Fishery Bulletin 105(2) Contents

Click on page numbers to go to PDF version of article.

Articles

161–167
Gentner, Brad
Sensitivity of angler benefit estimates from a model of recreational demand to the definition of the substitute sites considered by the angler

168–179
Anderson, Tara J., and Mary M. Yoklavich
Multiscale habitat associations of deepwater demersal fishes off central California

180–188
McClelland, Gary, and Jason Melendy
Use of endoparasitic helminths as tags in delineating stocks of American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence and Cape Breton Shelf

189–196
Hamilton, Judy, and Brenda Konar
Implications of substrate complexity and kelp diversity for south-central Alaskan nearshore fish communities

197–206
Ward, Rocky, Kevin Bowers, Rebecca Hensley, Brandon Mobley, and Ed Belouski
Genetic variability in spotted seatrout (*Cynoscion nebulosus*), determined with microsatellite DNA markers

207–233
Smith-Vaniz, William F., and Kent E. Carpenter
Review of the crevalle jacks, *Caranx hippos* complex (Teleostei: Carangidae), with a description of a new species from West Africa

234–248
Trites, Andrew W., Donald G. Calkins, and Arliss J. Winship
Diets of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, 1993–1999

249–265
Margulies, Daniel, Jenny M. Suter, Sharon L. Hunt, Robert J. Olson, Vernon P. Scholey, Jeanne B. Wexler, and Akio Nakazawa
Spawning and early development of captive yellowfin tuna (*Thunnus albacares*)

266–277
Zeller, Dirk, Shawn Booth, Gerald Davis, and Daniel Pauly
Re-estimation of small-scale fishery catches for U.S. flag-associated island areas in the western Pacific: the last 50 years

278–291
Somerton, David A., Peter T. Munro, and Kenneth L. Weinberg
Whole-gear efficiency of a benthic survey trawl for flatfish

Notes

292–295
Strange, Rex M., and Carol A. Stepien
Yellow (*Perca flavescens*) and Eurasian (*P. fluviatilis*) perch distinguished in fried fish samples by DNA analysis

296–304
Cooper, Daniel W., Katherine P. Maslenikov, and Donald R. Gunderson
Natural mortality rate, annual fecundity, and maturity at length for Greenland halibut (*Reinhardtius hippoglossoides*) from the northeastern Pacific Ocean

305–309
Roemer, Marja E., and Kenneth Oliveira
Validation of back-calculation equations for juvenile bluefish (*Pomatomus saltatrix*) with the use of tetracycline-marked otoliths

310–311
Guidelines for authors

312
Best Paper Awards

Subscription form

U.S. Department of Commerce
Carlos M. Gutierrez
Secretary

National Oceanic and Atmospheric Administration
Vice Admiral
Conrad C. Lautenbacher Jr., USN (ret.)
Under Secretary for Oceans and Atmosphere

National Marine Fisheries Service
William T. Hogarth
Assistant Administrator for Fisheries

Scientific Editor
Adam Moles, Ph.D.

Associate Editor
Elizabeth Siddon

Ted Stevens Marine Research Institute
Auke Bay Laboratories
Alaska Fisheries Science Center
17109 Pt. Lena Loop Road
Juneau, Alaska 99801

Managing Editor
Sharyn Matriotti

National Marine Fisheries Service
Scientific Publications Office
7600 Sand Point Way NE, BIN C1570
Seattle, Washington 98115-0070

Editorial Committee

Jeffrey M. Leis	Australian Museum, S
Thomas Shirley	Texas A&M Universit
David Somerton	National Marine Fishe
Mark Terceiro	National Marine Fishe

Sensitivity of angler benefit estimates from a model of recreational demand to the definition of the substitute sites considered by the angler

Brad Gentner

NMFS Office of Science and Technology
Fisheries Statistics and Economics Division
1315 East West Highway
Silver Spring, Maryland 20910

Email address: brad.genter@noaa.gov

Abstract—Fishery managers are mandated to understand the effects that environmental damage, fishery regulations, and habitat improvement projects have on the net benefits that recreational anglers derive from their sport. Since 1994, the National Marine Fisheries Service (NMFS) has worked to develop a consistent method for estimating net benefits through site choice models of recreational trip demand. In estimating net benefits with these models, there is a tradeoff between computational efficiency and angler behavior in reality. This article examines this tradeoff by considering the sensitivity of angler-welfare estimates for an increase in striped bass (*Morone saxatalis*) angling quality across choice sets with five travel distance cut-offs and compares those estimates to a model with an unrestricted choice set. This article shows that 95% confidence intervals for welfare estimates of an increase in the striped bass catch and keep rate overlap for all distance-based choice sets specified here.

Manuscript submitted 24 August 2005 to the Scientific Editor.

Manuscript approved for publication 7 August 2006 by the Scientific Editor.

Fish. Bull. 105:161–167 (2007).

Recreational angling is the second most popular outdoor sport nationwide when measured by number of participants. In 2004, 10.2 million anglers took 73.8 million recreational trips in the United States, exclusive of Alaska, Hawaii, and Texas (NMFS[1]). In addition to participation, anglers spend $20.4 billion dollars annually on trip-related and durable expenditures to pursue saltwater gamefish (Gentner et al., 2001), producing $30.5 billion in economic impacts and supporting nearly 350,000 jobs (Steinback et. al, 2004). Recreational fishing is an economically important activity and the National Marine Fisheries Service (NMFS) is mandated by law to examine changes in net benefits to anglers after the impact of environmental damage (oil spills, algal blooms, etc.), fishery regulations (bag limits, size limits, seasonal closures), and habitat improvement projects (damn removal, water quality improvements, etc.). Calculation of net benefits involves an examination of angler behavior when they make choices about taking recreational fishing trips.

Modeling angler trip demand involves observing anglers making recreation site choices and using a site choice model to estimate a recreational trip demand function. Site-choice models are typically estimated by using a random utility model (RUM). RUMs are used to estimate net benefits by looking at the cost of traveling to the site that anglers selected and comparing that cost to the cost of traveling to other sites in their choice set (set of sites considered by the angler). Without any other information about the site, these models allow one to estimate the net benefits of access to that site which can be used to examine closures due to environmental damages or regulation. If site-quality information is available, such as catch rates or other measures of environmental quality, the net benefits of those ecosystem services can be estimated as well.

Since 1994, it has been the goal of the NMFS to develop a consistent method for estimating recreational site-choice models to increase the speed and efficiency of meeting legal mandates. To this end, NMFS has sponsored a good deal of research into RUMs of recreational site choice to value site closures and angling quality (the quality of the angling experience as measured by catch and keep rates) (Haab and Hicks, 1999, Jones and Lupi, 1999, Parsons et. al, 1999). From this, and other work, the composition of an individual's choice set can impact net benefit estimates, giving rise to several difficulties when modeling angler net benefits. First, NMFS's RUM models concentrate on only single day trips, because it is difficult to disentangle the value of angling for anglers on trips that have

[1] NMFS (National Marine Fisheries Service). 2006. Fisheries Statistics and Economics Division. Marine Recreational Fisheries Statistical Survey Real Time Data Queries. Website: http://www.st.nmfs.gov/st1/recreational/database/queries/index.html (accessed on 13 August 2006).

multiple purposes. Because focus is strictly on single day trips, it would be incorrect to include sites in an angler's choice set if those sites are "too far" for the angler to consider when choosing a site for a single day trip. Second, a large number of sites in each individual's choice set can be computationally costly, particularly when a nested choice structure is appropriate, and increase the time it takes to bring policy analyses to the table. This problem may indicate that there is a tradeoff between computational efficiency and angler behavior in reality; a balance that will be examined here.

There is literature on the specification of choice sets based on many factors including distance. Parsons and Hauber (1998) estimated a freshwater recreational angler site choice model and found that there is little difference in the magnitude of welfare effects as one reduces the spatial scope of choice sets until a threshold of 1.6 hours one-way travel time is reached. This spatial scope translates into 32 mile and 80 mile distance thresholds, if one assumes a 20 mile per hour (mph) urban travel speed and a 50 mph highway travel speed, respectively. Below that threshold, welfare estimates inflate as the constraint tightens. Whitehead and Haab (1999) estimated a site choice model using a range of choice sets constructed with distance and site-quality metrics. They found that there is very little difference in the trip cost coefficients across distance-based choice sets that eliminate between 13% and 82% of the available sites. Hicks and Strand (2000) found that because the probability of choosing a site depends on the choice set, the likelihood function is also dependent on the choice set. If the choice set is incorrect, biased parameter estimates could be a consequence. The welfare estimates derived in the "Materials and methods" section below explicitly include the choice set and demonstrate this interaction.

This analysis will examine the sensitivity of welfare estimates in a RUM model of recreational demand across six distance-based definitions of site choice. This analysis will focus on a single species, striped bass (*Morone saxatalis*), from a single mode (the private rental boat mode) to avoid a nested choice structure. A simulation approach will be used to derive confidence intervals around these estimates in order to examine the significance of any differences found and to expand the literature that has previously been focused on only on the magnitude of the differences in welfare estimates.

Materials and methods

An angler chooses a fishing site from the set of all alternative sites if the utility of visiting that site is greater than the utility of visiting any other site in the global choice set. Denoting the set of all alternatives faced by any angler by $S = \{1, \ldots, N\}$ as the choice set, the indirect utility of visiting site j is

$$U_j(q_j, y-p_j, \varepsilon_j) = V_j(q_j, y-p_j) + \varepsilon_j, \quad (1)$$

where U_j = an individuals utility;
V_j = the deterministic portion of utility;
y = income;
p = the cost of angling at site j;
q = a vector of characteristics of site j; and
ε_j = the unobservable portion of indirect utility.

In the RUM framework, an angler will choose site j from S if

$$V_j(q_j, y-p_j) + \varepsilon_j \geq V_k(q_k, y-p_k) + \varepsilon_k, j \in S, \forall k \in S, \quad (2)$$

where the indirect utility of visiting site j is greater than the indirect utility of visiting site k for all k in the global choice set, S.

The random portion of the random utility model stems from the unobservable portion of indirect utility, captured here in the error term ε_j. If this error term is assumed to be distributed in a type-I extreme value distribution, the above site choice framework can be modeled with the conditional logit model. Maddala (1983) has provided a complete derivation of the conditional logit model. Within this framework, the probability that i visits site j is given by

$$P_i(j) = P(j \mid j \in S) = \frac{e^{V_j(q_j, y-p_j)}}{\sum_{k \in S} e^{V_k(q, y-p_k)}}. \quad (3)$$

Up to this point it has been assumed that each angler faces the same choice set, S. This is not a necessary assumption and can be generalized to represent the possibility that i faces a choice set S_i that is a subset of the global choice set S. In this case the indirect utility comparison becomes

$$V_j(q_j, y-p_j) + \varepsilon_j \geq V_k(q_k, y-p_k) + \varepsilon_k, j \in S, \forall K \in S_i, \; _i \subset S \quad (4)$$

and the probability that angler i chooses site j becomes

$$P_i(j) = \frac{e^{V_j(q_j, y-p_j)}}{\sum_{k \in \; _i} e^{V_k(q, y-p_k)}}. \quad (5)$$

Because the goal of the present study is to examine the sensitivity of welfare estimates of a quality change to the specification of choice sets, it is necessary to show how the choice set enters the calculation of compensating variation (CV), or the level of income required to keep the angler at the same level of expected utility after the quality change. The following expression for CV is taken from the work of Bockstael et al. (1991), who examined the value of quality improvements in the demand for recreation, where β_y is the travel cost parameter.

$$CV = \frac{\ln\left(\sum_{k \in \; _i} e^{v_k(q_k^1, p)}\right) - \ln\ln\left(\sum_{k \in \; _i} e^{v_k(q_k^0, p)}\right)}{\beta_y} \quad (6)$$

The summation of the indirect utilities is across the choice set facing each individual, S_i, and not the global choice set, S.

Since 1979, data have been collected on marine recreational angling during the Marine Recreational Fishery Statistics Survey (MRFSS). The MRFSS consists of two independent but complementary surveys: a field survey and a telephone survey, conducted annually in six two-month "waves." The field survey is an intercept survey of anglers conducted at fishing access sites and is designed to obtain a random sample of recreational trips for computing catch per unit of effort. Fish retained by interviewed anglers are sampled for length and weight. Fish not retained by the angler are not observed, but count data on this unobserved catch are collected. The data on harvest provide a picture of the size distribution of the kept fish from the stock. If a fishery is regulated by a minimum size limit, a catch-and-keep rate calculated from these data indicates the catchability of fish large enough to keep. As such, it is the observed rate at which anglers can catch and keep fish from a stock.

The intercept sample is stratified by state, wave, fishing mode, fishing area, catch type, and species. Specific data elements collected during the intercept survey include state, county, and zip code of angler's residence, hours fished, primary area fished, target species, gear used, and days fished in the last two and 12 months. During the intercept portion of the survey, data are collected on the length and weight of all fish species retained by the angler and the species and condition of all catch not retained by the angler. Upon completion of the base MRFSS, anglers in the Northeast (NE) (Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Delaware, Maryland, and Virginia) were asked to complete a short add-on questionnaire in 2000. This questionnaire provided information on whether or not the trip was a single-day or longer trip and, if it was a multiple-day trip, whether fishing was the primary purpose of the trip. Data were also collected on the angler's saltwater fishing experience (in number of years), boat ownership (whether owned or not), and whether or not the individual took time off without pay to take the fishing trip. If the individuals responded in the affirmative to the later, they were asked the number of hours in their work week and their personal income. The survey instrument is available at the NMFS web site (NMFS[2]).

In order to reduce the complexity of the modeling effort, the angler's choice to fish rather than participate in some other recreational activity, the angler's choice to fish in a private or rental boat mode, and the angler's decision regarding a species target are exogenous to the model. Because the area fished is not documented in the MRFSS, a fishing site is defined as the point of fishing access. As mentioned previously, the treatment of all substitute sites can be quite costly from a data standpoint for a number of reasons. Because thousands of individual sites in the North East (NE) region are recognized in the MRFSS, estimation can be a lengthy process, particularly with nested models. In addition, not all species are sampled in all survey waves at all sites in all modes; therefore the calculation of historic catch rates at the individual site level results in many empty cells. To speed estimation and to fill some of these empty cells, all sites within a coastal county were aggregated into one site that represented that county. Across the NE, there are roughly 63 coastal counties, and therefore 63 sites. In order to examine whether this aggregation strategy induces any bias into the estimation of the conditional logit model, a variable (m) was created that represents the number of MRFSS sites aggregated into each new site. The rule that a county equals a site was not strictly followed in all cases. Some geographically diverse counties (i.e., those counties with both ocean frontage and bay frontage) were separated into two sites because of the different opportunities provided by these different types of water.

Both the historic five-year average catch rate (catch rate) and catch-and-keep rate (KRATE) were calculated for the boat mode for each wave and site combination. KRATE measures the catchability of a striped bass large enough to keep, incorporating the five-year average probability of catching a striped bass large enough to keep. The distinction between the catch rate and KRATE is particularly important for striped bass because this species is heavily regulated. Historic KRATE was used in the model because it represents the portion of the catch that an angler would be able to keep, not just the increase in overall catch. It is also the measure of angler quality used in the Whitehead and Haab (1999) study. Even after the site aggregation, some counties did not contain enough data points on striped bass catch from the boat mode over the 5-year period.

Whitehead and Haab (1999) replaced missing catch rates using the catch rate from the nearest neighboring site in some cases and with zero values, in other cases depending more or less on mode. Hicks et al. (1999) recognized this approach to be *ad hoc* and estimated his model using both nearest neighbor and zero value assignment, another *ad hoc* approach, and found that the treatment of missing values did not significantly affect the welfare estimates. He concluded that the zero assignment is perhaps less arbitrary because the empty cells actually convey information. That is, if there are no observations of average catch within a particular wave+mode+site+species combination, the site is not very productive over that combination. As a result, zero assignment requires less judgment by the researcher; therefore that is the approach used here.

Estimating any demand equation requires a price variable. Because recreational fishing experiences are not openly traded in markets, travel cost (both the actual cost of travel plus the opportunity cost of time) is

[2] NMFS (National Marine Fisheries Service). 2006. Fisheries Statistics and Economics Division. Survey Instruments. Website: http://www.st.nmfs.gov/st1/econ/surveys/survey_timeline.html (accessed on 13 August 2006).

used as the price. Round-trip travel cost (*ttc*) is calculated as the following;

$$ttc = (\ 0.33 \times distance \times 2) + \left(\frac{(distance \times 2)}{40} + hrsf\right) \times lost\_income \times w, \quad (7)$$

where *distance* = the one-way distance from the anglers home zip code to the zip code, or latitude/longitude, of the intercept site.

This distance is multiplied by the Federal Travel Regulations reimbursement rate for private transportation ($0.33) and includes both the fixed and variable costs of operating an automobile. The variable *lost_income* is a dummy that takes the value of 1.0 if the individual did take time off work without pay to go fishing. If the individual lost income, their wage rate (w) is multiplied by the travel time plus the time on site (*hrsf*) and this amount is added to the travel cost (40 miles per hour is used as the average travel speed). Therefore, the opportunity cost of onsite time and travel time is only included if an individual took time off work to participate in fishing on a given day. If the individual is not losing income for the trip, his travel cost is simply round-trip distance multiplied by the fixed and variable costs of operating an automobile. As is typical for these MRFSS data sets, very few anglers (3.34%) report having foregone income to take the trip. To account for the opportunity cost of time for those anglers not losing income, travel time is used as a measure of time cost for those individuals. In order not to double count those that lost income taking a trip, the expression for travel time (*tt*) is

$$tt = \left(\frac{(distance \times 2)}{40}\right)(1 - lost\_income). \quad (8)$$

Keeping only those anglers that have targeted or caught striped bass from the boat mode on a single day trip leaves 3630 usable observations.

With an aggregation strategy in place and the variables defined, the estimation of the conditional logit model follows. As a reminder, the choice of whether or not to take a fishing trip, which mode to fish in, and what species to pursue are made outside of this model. The angler then chooses the site that maximizes indirect utility from his or her set of substitutes. Every model carries a set of implicit assumptions. Angler behavior within this model is defined on a trip-by-trip basis and the angler is not allowed to modify the number of trips taken each season. Therefore, each choice is independent of the next, and unobservable utility, ε_j, is independent of any other trips. Additionally, the MRFSS intercept survey is assumed to approximate a random sample of trips. The author acknowledges these contentions with choice-based sampling in the MRFSS data, and this is an area of research that this author and NMFS scientists continue to explore.

Variables in the deterministic portion of indirect utility include travel cost (*ttc*), travel time (*tt*), log of the number of MRFSS intercept sites aggregated into the county site used in the model (m), and historic KRATE per trip for striped bass at site j (q_j). Indirect utility is

$$\beta_c tt_{ij} + \beta_q q_j + \beta_t t_{ij} + \beta_m \ln(m_j) + \varepsilon_j. \quad (9)$$

With this expression for indirect utility, the probability that angler i selects site j is

$$P_i(j) = \frac{e^{\beta_c tt_{ij} + \beta_q q_j + \beta_t t_{ij} + \beta_m \ln(m_j)}}{\sum_{k \in i} e^{\beta_c tt_{ik} + \beta_q q_k + \beta_t t_{ik} + \beta_m \ln(m_k)}} \quad (10)$$

and the expression for the change in compensating variation for a change in the historic catch and keep rate, after assuming a constant marginal utility of income, is the following:

$$\frac{1}{\beta_c}\left(\begin{array}{l}\ln\left(\sum_{j \in S_i} \beta_c tt_{ij} + \beta_q q_j^0 + \beta_t t_{ij} + \beta_m \ln(m_j)\right) \\ -\ln\left(\sum_{j \in S_i} \beta_c tt_{ij} + \beta_q q_j^1 + \beta_t t_{ij} + \beta_m \ln(m_j) + \varepsilon_j\right)\end{array}\right), \quad (11)$$

where q^0 = the historic KRATE; and
q^1 = the KRATE after the environmental or policy change.

Table 1 provides descriptive statistics for all the variables to be used in the analysis and some angler-specific attributes in order to give the reader some background on these anglers. Throughout the range of this data collection, the bag limit for striped bass is two fish per day. On average, anglers catch far less than the limit. In fact, the base catch rate for anglers targeting or catching striped bass from the boat mode is less than one fish per trip. What is readily apparent is that there are some irrational anglers in this group, at least concerning travel time. The maximum travel time translates into a 798 mile one-way travel distance, which does not seem feasible for a one-day trip. Even after eliminating those anglers that admit to taking an "overnight" trip, there are obviously anglers that are away from home longer than 24 hours. One explanation is that these anglers live in the local area seasonally and have given the zip code of their permanent address, which is used to calculate travel distance. Another explanation arising from the author's experience in the field is that some of these anglers drive incredibly long distances and fish for 24 or more hours. They do not consider their trip to be an overnight trip because they are not staying in a hotel even though their round trip travel distance indicates that they were away from home for more than 24 hours. There were only 3 individuals in the data set with one-way travel distances greater than 500 miles and the results were not sensitive to leaving these outliers in the model. As a result they remain in the data set. Other statistics of note include the variable that

Table 1

Descriptive statistics for selected variables describing angler and trip characteristics from the only data set used in this study from the 2000 Marine Recreational Fisheries Statistical Survey economic add-on survey conducted in Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut, New York, New Jersey, Delaware, Maryland, and Virginia.

Variable	Mean	Standard deviation	Minimum	Maximum
Used in model				
Travel cost (*ttc*) (US$)	30.39	38.36	0.0	778.73
Travel time (*tt*) (hours)	1.99	2.15	0.0	39.93
Aggregation variable (*m*) (number of sites)	43.85	37.88	5.0	138.00
Catch-and-keep rate (*q*)	0.19	0.40	0.0	2.00
One-way travel distance (*distance*) (miles0miles)	41.54	43.13	0.1	798
Not used in model				
Boat ownership (%)	0.73	0.44	0.0	1.00
Hours fished	4.20	1.88	0.5	22.00
Years fished	23.61	14.76	0.0	70.00
Catch rate (no. of fish)	0.89	1.64	0.0	10.67

looks at the aggregation of sites. On average there are almost 44 MRFSS intercept sites aggregated into the definition of a "site" used in the present study and a maximum of 138 sites and a minimum of five sites in a county. On average, anglers spend 4.2 hours on the water and 73% own the boat they are fishing from. Finally, this is a fairly experienced group, with an average of almost 24 years of saltwater fishing experience.

The final portion of this analysis yet to be discussed is the definition of distance-based choice sets. Haab and Hicks (1997) and Parsons and Hauber (1998) found that welfare estimates change little beyond a certain threshold. Up to a point, limiting an angler's choice set by using a distance-based metric only increases the realism of the choice that anglers consider in reality. Hicks et al. (1999) used such a designation in their analyses. Both included all sites within 150 miles, if the angler lived within 30 miles of the site selected, and all sites within 400 miles otherwise. The extreme rational limit for a one-day trip is probably 400 miles one-way. That distance translates into a 10 hour or 6 hour and 40 minute one-way travel time at 40 and 60 miles per hour, respectively. Whitehead and Haab (1999) used definitions of distance-based choice sets that ranged from 180 miles one-way to 360 miles one-way (3–6 hours one-way at 60 miles per hour), realizing that the 360 mile cut-off is likely not very realistic. These definitions probably drive the small difference in parameters across specifications, because eliminating sites outside of what anglers are really considering should have little effect (Whitehead and Haab, 1999).

To examine the definition of choice sets, this study examined much smaller cut-offs than those found in the previous literature that focused on saltwater angling. The cut-offs included the following: a full unrestricted choice set, and 300-, 250-, 200-, 150-, and 100-mile distance cut-offs. Initially, a 50-mile one-way distance cut-off was included, but, because of the site aggregation strategy used, the only substitutes left in the choice set at the 50-mile cut-off were closer than the site that was chosen, for most anglers. If it is possible to estimate the model on an individual site basis, it would be possible to run smaller distance cutoffs without encountering this problem. In order not to also drop observations when applying these cut-offs, if an individual was observed to make a choice outside of the cut-off, that observation is retained. If all substitute sites for that individual are also outside of the cut-off, the next nearest site is included in that angler's choice set. Therefore, anglers have at least one substitute left in their choice set, no matter how restrictive the cut-off becomes. The average number of sites in each choice set is 63, 37.2, 30.5, 23.3, 16.9, and 10.6 for the six choice sets, from least restrictive to most restrictive, respectively. In percentage terms, these restrictions on the choice set eliminate between 40% and 93% of the available sites.

Estimation of the confidence intervals around these welfare estimates is calculated by taking 1000 random draws from a multivariate normal distribution parameterized by the vector of estimated parameters and their covariance matrix. Sorting these draws from highest to lowest and removing the upper and lower 2.5% and 5%, respectively, construct 95% and 90% confidence intervals (Krinsky and Robb, 1986).

Results

Table 2 contains the parameter estimates and standard errors of the six conditional logit models. All six models strongly reject the hypothesis that the coefficients are simultaneously equal to zero. Also, all coefficients in all models are statistically significant at the 99% level or better. In general, anglers prefer sites that are closer to home, both in terms of the cost of driving and the time cost (travel time multiplied by the individual's

Table 2

Parameter estimates for the six distance-based conditional logit models (standard errors in parantheses).

	Choice set					
Variable	Full	300-mile	250-mile	200-mile	150-mile	100-mile
Travel cost (*ttc*)	0.06242	−0.06240	−0.06232	−0.06176	−0.05827	−0.04150
(US$)	−(0.00573)	(0.00573)	(0.00575)	(0.00582)	(0.00606)	(0.00682)
Travel time (*tt*)	−0.23226	−0.23154	−0.23216	−0.23771	−0.27057	−0.36472
(hours)	(0.07753)	(0.07759)	(0.07782)	(0.07873)	(0.08186)	(0.09201)
Log of aggregation variable (*m*)	0.68125	0.68220	0.68262	0.68293	0.68187	0.67143
(no. of sites)	(0.02482)	(0.02483)	(0.02484)	(0.02484)	(0.02484)	(0.02479)
Catch-and-keep rate (*q*)	0.67653	0.67535	0.67584	0.67506	0.66885	0.65325
(no. of fish)	(0.03792)	(0.03794)	(0.03795)	(0.03795)	(0.03794)	(0.03820)
LR[1]	17,245.31	13,192.55	11,695.28	9695.16	7350.95	3891.39
R^2[2]	0.573	0.507	0.523	0.430	0.364	0.236

[1] Value of the likelihood ratio (LR) statistic testing the hypothesis that all betas = 0.
[2] McFadden's psuedo R^2.

wage rate). Additionally, anglers prefer sites that offer the possibility of catching and keeping more striped bass. Finally, with regard to the number of MRFSS sites aggregated into a site as defined in this study, anglers preferred to visit counties that contain more sites. Table 3 gives the mean CV for a one-fish increase in the catch-and-keep rate. A one-fish increase in the catch-and-keep rate is equivalent to the net benefits of an improvement in angling quality large enough to increase the keep rate by one fish or a regulation that allows increasing keep rates. A quality change significant enough to change KRATE by one fish would be unrealistic in the short term, considering the striped bass stock size distribution inferred from the catch rate and KRATE estimates (Table 1). Because KRATE incorporates the five-year average probability of catching a striped bass large enough to keep, this one-fish increase in KRATE models an angler's willingness to pay for a one-fish increase in the bag limit or an angler's willingness to pay for a special license allowing the retention of one striped bass more than the current two-fish limit.

This result supports Parson and Hauber's (1998) and Whitehead and Haab's (1999) results that there is indeed little difference in the definition of choice sets with the use of a distance metric. To examine the significance of the difference in welfare estimates, and not just the magnitude, 95% confidence intervals were calculated around each welfare measure (Krinsky and Robb, 1986). In fact, the mean of the smallest choice set is almost entirely contained within the 95% confidence interval of the next smallest choice set, and the entire lower bound for the smallest choice set is contained in the next smallest choice set. This is demonstrated graphically in Figure 1. From Figure 1, however, it appears that as the choice sets are truncated past the 150-mile threshold, welfare estimates rise—a similar result to that of Parson and Hauber (1998). Unfortunately, the aggregation strategy necessary when using the MRFSS data precludes an examination of a distance-based cut-off as small as that used in Parsons and Hauber's study (1998).

Table 3

Mean increase in angler benefits, measured by compensating variation (with 95% and 90% confidence intervals [CIs], for a one-fish increase in the catch-and-keep rate by distance-based choice set).

		95% CI		90% CI	
Choice set	Mean increase	Upper	Lower	Upper	Lower
Full	$10.84	$13.56	$8.89	$13.05	$9.15
300-mile	$10.82	$13.57	$8.86	$13.04	$9.13
250-mile	$10.84	$13.61	$8.90	$13.29	$9.18
200-mile	$10.93	$13.79	$8.95	$13.30	$9.23
150-mile	$11.48	$14.73	$9.28	$14.22	$9.57
100-mile	$15.74	$23.57	$11.65	$22.05	$12.23

Conclusions

In general, as choice sets are restricted, the coefficient on cost goes up, its absolute value goes down, and its standard error goes up, but only slightly, until the point is reached where the aggregation strategy begins to impose an artificial restriction on the choice set with this data

set. It would be interesting to examine the effect of the aggregation strategy by using the individual MRFSS intercept sites. It is possible that using average catch-and-keep rates calculated over a longer time series would result in far fewer empty cells, which are the main hurdle to using the individual MRFSS sites.

Mean one-way travel distance in the data set is 41.5 miles (Table 1). All of the choice sets at and above the 150 mile cut-off have an almost equal proportion of sites in the choice set and sites chosen at the cut-off point. That is, the percentage of substitutes within the cut-off and the percentage of sites chosen within the cut-off are equal (near 99% for both) for the full, 300-, 250-, and 200-mile choice sets. At the 150 mile cut-off this equality begins to fail and the percentage of chosen sites inside the cut-off fall to 98% and 94% for the 150- and 100-mile cut-offs, respectively. This fall is being driven partially by the aggregation strategy. Although this result has not been examined by the author, it is likely that the average distance for an angler to travel outside his county of residence is somewhere between 100 and 150 miles. Again, if the historic catch rate could be calculated to examine individual MRFSS sites, this aggregation restriction could be examined to determine the overall sensitivity of welfare estimates to the designation of distance-based choice sets.

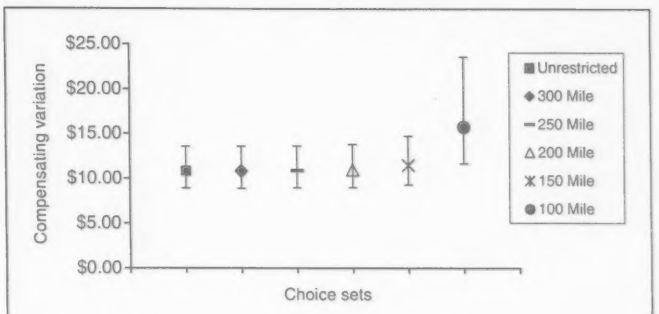


Figure 1

Mean benefits as measured by compensating variation (with 95% confidence intervals) for a one-fish increase in the catch-and-keep rate by distance-based choice set.

In conclusion, when estimating the net benefits of quality changes for recreational anglers with the MRFSS data, it matters little how restrictive the choice sets become with a distance metric, as long as the researcher does not ask more of the aggregation strategy than it can provide. This result quantifies the significance of the difference in welfare estimates across aggregation strategies and indicates the strengths and the weaknesses of a nationwide data set on marine angling in estimating net benefits and thus makes policy analysis quicker and easier.

Literature cited

Bockstael, N. E., K. E. McConnell, and I. E. Strand.
1991. Recreation. *In* Measuring the demand for environmental quality (J. Braden, and C. Kolstad, eds.), 227–268 p. North-Holland Publs., Amsterdam, The Netherlands.

Gentner, B. J., S. Steinback, and M. Price.
2001. Marine angler expenditures in the Pacific coast region, 2000. NOAA Tech. Memo. NMFS-F/SPO-49, 66 p.

Haab, T., and R. Hicks.
1997. Accounting for choice set endogeneity in random utility models of site choice. J. Environ. Econ. Manage. 34:127–47.

Haab, T., and R. Hicks.
1999. Choice set considerations in models of recreation demand. Mar. Res. Econ. 14:271–281.

Hicks, R., A. B. Gautam, D. VanVoorhees, M. Osborn, and B. Gentner.
1999. *Thalassorama*: an introduction to the NMFS marine recreational fisheries statistical survey with an emphasis on economic valuation. Mar. Res. Econ. 14:375–385.

Hicks, R., and I. E. Strand.
2000. The extent of information: Its relevance for random utility models. Land Econ. 76:374–385.

Jones, C. A., and F. Lupi.
1999. The effects of modeling substitute activities on recreational benefit estimates. Mar. Res. Econ. 14:357–374.

Krinsky, I., and A. L. Robb.
1986. On approximating the statistical properties of elasticities. Rev. Econ. Stats. 68:715–719

Maddala, G. S.
1983. Limited dependent and qualitative variables in econometrics, 401 p. Economic Soc. Monographs. Cambridge Univ. Press, New York, NY.

Parsons, G. R., D. M. Massey, and T. Tomasi.
1999. Familiar and favorite sites in a random utility model of beach recreation. Mar. Res. Econ. 14:299–315.

Parsons, G. R., and A. B. Hauber.
1998. Spatial boundaries and choice set definition in a random utility model of recreation demand. Land Econ. 74:32–48.

Steinback, S., B. Gentner, and J. Castle.
2004. Economic impacts of marine recreational angling in the United States. U.S. Dep. Commer., NOAA Prof. Pap. NMFS 2, 169 p.

Whitehead, J. C., and T. C. Haab.
1999. Distance and catch based choice sets. Mar. Res. Econ. 14:283–299.

Multiscale habitat associations of deepwater demersal fishes off central California

Tara J. Anderson (contact author)
Mary M. Yoklavich

Email address for T. J. Anderson: t.anderson@aims.gov.au

Fisheries Ecology Division
Southwest Fisheries Science Center
National Marine Fisheries Service
110 Shaffer Road,
Santa Cruz, California 95060
Present address (for T. J. Anderson): Australian Institute of Marine Science
PMB 3 Townsville MC
Queensland 4810, Australia

Abstract—Fish-habitat associations were examined at three spatial scales in Monterey Bay, California, to determine how benthic habitats and landscape configuration have structured deepwater demersal fish assemblages. Fish counts and habitat variables were quantified by using observer and video data collected from a submersible. Fish responded to benthic habitats at scales ranging from cm's to km's. At broad-scales (km's), habitat strata classified from acoustic maps were a strong predictor of fish assemblage composition. At intermediate-scales (m's–100 m's), fish species were associated with specific substratum patch types. At fine-scales (<1 m), microhabitat associations revealed differing degrees of microhabitat specificity, and for some species revealed niche separation within patches. The use of habitat characteristics in ecosystem-based management, particularly as a surrogate for species distributions, will depend on resolving fish-habitat associations and habitat complexity over multiple scales.

Manuscript submitted: 16 June 2006 to the Scientific Editor.

Manuscript approved for publication 17 August 2006 by the Scientific Editor.

Fish. Bull. 105:168–179 (2007).

Measuring fish-habitat associations on a number of spatial scales is essential in determining the relative importance of habitat types and landscape configuration in structuring fish assemblages and populations. Many benthic habitat characteristics (e.g., substratum type, depth, relief) are important in explaining the local distribution and abundance patterns of demersal fishes (e.g., Jones and Syms 1998; Stephens et al., 2006). An organism's use of habitat may also change as a function of scale (Wiens, 1989). For example, fishes may make a considerable range of choices about their occupancy of specific habitats and may sample their environment at a range of spatial and temporal scales (Ault and Johnson, 1998; Syms and Jones, 1999). Habitat types (abiotic and biotic), however, are found within a large spatial domain (landscape) in which the configuration and connectivity between neighboring habitat areas may contribute to population structure (Forman, 1995). For example, landscape configuration and the degree of habitat patchiness may modify the distribution and movement of an organism, and the interactions among species (Addicott et al., 1987).

On the U. S. West Coast, demersal fishes, particularly rockfishes (*Sebastes*) are a dominant feature of the benthic ecosystem (Love and Yoklavich, 2006) and are important for both commercial and recreational fisheries (Love, 2006). At broad spatial scales, traditional trawl surveys have documented a range of biogeographical and depth patterns for harvested demersal species (Gunderson and Sample, 1980; Weinberg, 1994; Williams and Ralston, 2002). Less research has been done on the role that benthic habitat variables, such as substratum type and relief, play in explaining the distribution and abundance of either commercial or noncommercial species. Strong relationships between demersal fish species and a range of habitat characteristics, particularly substratum type and abundance of giant kelp, have been identified in shallow (<30 m) coastal waters (Stephens et al., 2006). However, many demersal species in this system, particularly rockfish species, are found over extensive depth ranges beyond those that can safely be investigated with SCUBA (Love et al., 2002). The use of submersibles and remotely operated vehicles (ROVs), with sampling protocols similar to those of nearshore surveys (Stein et al., 1992; Adams et al., 1995; Yoklavich et al., 2000), provides the capabilities to make quantitative *in situ* observations of fish-habitat associations in deepwater (>30 m). Studies in which these tools are employed are also beginning to demonstrate characteristic habitat associations for deepwater demersal fish species (Love and Yoklavich, 2006). The importance of spatial scale in un-

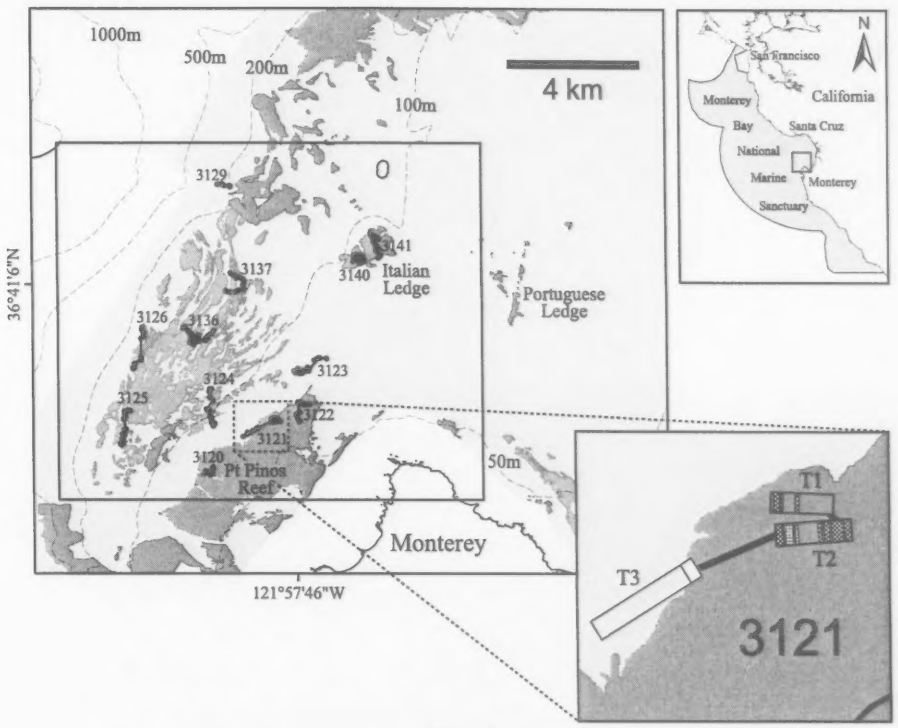


Figure 1

Seafloor map of the continental shelf in southern Monterey Bay, central California, depicting the three acoustically derived broad-scale strata and *Delta* submersible sampling locations (dive numbers 3120–3141). Hard substratum (i.e., complex outcrops) is depicted as dark gray areas. Mixed substratum (areas of hard mixed with soft) is depicted as medium gray areas. Soft substratum (i.e., areas of contiguous soft sediments) is depicted as light gray areas. White areas were not surveyed; box = 10×12 km study area. Bottom insert is an example of the observed intermediate-scale substratum types recorded within the three transects of dive 3121 (depicted by the three rectangles T1=transect 1, T2=transect 2, and T3=transect 3) in relation to the seafloor map of that area. Transects sampled in hard substratum (T1 and T2) were heterogeneous and were composed of mixed patches dominated by rock (dark gray), boulders (diagonal hatching) and cobbles (light gray checks). In contrast, transects run within soft substratum (T3) were more homogeneous, composed of either sand (white) or mud (light gray).

derstanding these associations, however, has received much less attention (Langton et al., 1995).

In this study, we examined the relationship between deepwater demersal fishes and benthic habitat variables at three spatial scales in an area encompassing a proposed marine protected area (MPA) in southern Monterey Bay, California. At the broad spatial scale of km's, habitat strata were identified from acoustic seafloor maps. Within these strata we conducted submersible transects and recorded both benthic habitat variables—such as substratum type, depth, relief, and habitat patchiness—and fish abundance and size. At the intermediate scale of 10–100's of meters, within-transect habitat measures, in combination with fish counts, provided measures of habitat patchiness and fish use of these patches. Finally, we assessed fine-scale or microhabitat (<1 m) fish-habitat associations by recording the habitat type located directly beneath each fish. These multiple spatial scales of habitat association were integrated to examine multiscale habitat and landscape requirements of these species.

Material and methods

Survey of fish habitat

To quantitatively sample demersal fishes and benthic habitats on the continental shelf in southern Monterey Bay (36°E, 121°S) (Fig. 1), *in situ* counts and habitat characterizations were made from the two-person *Delta* submersible. The submersible survey was conducted

from 9 through 12 October 1993 (boreal fall), between the hours of 07:30 (1 hour after sunrise) and 17:00 (1 hour before sunset). Thirty-three strip-transects (2 m wide by 10 minutes in duration) were surveyed within a 10×12 km study area (Fig. 1). During each transect, the scientific observer made observations from the central starboard porthole while the pilot drove the submersible about 1 m above the seafloor at a speed of 0.4–0.9 knots depending on currents and topography. Three broad-scale strata (hard, mixed, soft substratum), which had been identified from seafloor maps by using geophysical data (Eittreim et al., 2002; Anderson et al., 2005), were sampled at depths ranging from 72 to 252 m.

Within each 10-minute transect, all demersal fishes within 2 m of the submersible were identified to the lowest taxon, measured (total length was visually estimated to 5-cm size classes), and counted vocally by the scientific observer. An external starboard mounted Hi-8 video camera simultaneously recorded the seafloor along each transect and the scientific observers' vocal commentary on the audio track. A hand-held sonar gun was used to gauge transect width, and paired lasers, set 20 cm apart and projected into the observers' field of view, were used to gauge fish size. A *Pisces Video Plus II* data-logger (*Pisces Design*, San Diego, California) superimposed time, date, depth, and altitude of the submersible onto the video image. Final fish sizes and counts were derived from the videotape, by using the audio commentary as supporting information. All video analyses were conducted by the same person to reduce between-observer variability. Individual fish that could not be distinguished to species were assigned to a taxonomic group, for example: to subgenus (e.g., young-of-year *Sebastes* spp. [YOY], *Sebastomus* spp. [rosy-like rockfish species]), genera (e.g., *Citharichthys* spp. [sanddabs], *Zaniolepis* spp. [combfishes]), family (e.g., Agonidae [poachers], Cottidae [sculpins]) or order (e.g., Pleuronectiformes [flatfishes]).

Benthic habitat characteristics within each transect (intermediate scale) were categorized and delineated from the videotape. Substratum composition (rocks, boulders [>25.5 cm], cobbles [6.5–25.5 cm], sand, and mud) within a patch was categorized by using the dominant (primary=>50%) and subdominant (secondary=>20%) percentages of substratum cover used by Stein et al. (1992) and Yoklavich et al. (2000). For example, a patch comprising >50% rock and >20% boulders was classified as rock-boulder (RB); a patch comprising >70% rock was classified as rock-rock (RR). Patches were delineated from videotape where patch duration exceeded 3 seconds of elapsed video time (i.e., where patch size >1.7 m). Habitat relief within each patch was categorized as flat (0–5°), low (5–30°), or high (>30°). These methods adequately defined intermediate scale habitat composition and patchiness within transects (i.e., m's–100's m), yet logistically enabled long transects (max. 585 m) to be quantified. To describe fine-scale (<1 m) microhabitat use by demersal fish species, we recorded the type of substratum (rock, boulders, cobbles, sand, or mud) directly beneath each fish. This multiscale approach enabled habitat associations at each scale to be recorded independently of associations at other scales.

Transect length, independent of submersible speed, was estimated by using the known distance between the lasers (i.e., 20 cm) as a ruler, by counting the number of lengths that occurred sequentially over a 15-s duration within each minute of videotape, and then multiplying by transect duration (i.e., 10 min). Patch lengths were calculated by using the same method but were multiplied by patch duration (elapsed time per patch).

Analysis

The categorical measures of substratum type were recoded as semiquantitative variables. Primary and secondary categories were recoded so that each substratum type within a patch was given a percent cover value of 0%, 20%, 50%, or 70%. For example, rock-rock (RR) was recoded as 70% rock (50%+20%) while all other substratum types scored a value of 0%; similarly boulder-cobble (BC) was recoded as 50% boulder, 20% cobble and all other types scored a value of 0%. Habitat relief was recategorized as an ordinal variable with values of 1, 2, and 3 that corresponded with flat, low, and high relief. The mean and standard error for substratum types and relief, and median depth were then calculated for each transect (broad-scale) and patch (intermediate-scale). Habitat patchiness at the broad-scale was represented by "patch number"—the number of patches within each transect, and "patch size"—calculated as the log(*patch length*) within each transect. Benthic habitat variables, with the exception of patch number and patch size, were $x^{0.5}$ transformed to improve data normality and linearity between variables. Principal components analysis (PCA) was run on the correlation matrix of the transformed transect-level data to evaluate the validity of the broad-scale strata classifications and to describe the relationship between benthic habitat variables over broad spatial scales.

To examine the relationship between fish and habitat, total abundance and species richness were calculated for all fish species and rockfish species at both transect (transect length×2 m width) and patch (patch length×2 m) scales: fish densities were then expressed as numbers per 1000 m^2 (transects), and 200 m^2 (patches). To examine the fish assemblage in relation to harvest potential, we classified species as either commercial (e.g., *Sebastes paucispinis* [bocaccio], *S. ruberrimus* [yelloweye rockfish], *S. flavidus* [yellowtail rockfish], *Ophiodon elongatus* [lingcod], and *Microstomus pacificus* [Dover sole]) or noncommercial (e.g., *S. wilsoni* [pygmy rockfish], *Rhinogobiops nicholsii* [blackeyed goby], and *Zaniolepis* spp.). We also categorized fishes as small (≤20 cm) or large (>20 cm). Individual species and taxon groups were included in analyses when they were present in more than 5% of all patches. Consequently, 21 taxa (15 species and six groups) from nine families were retained for analyses. The data on fish distributions were examined by using histograms and Taylor power

plots (i.e., log(*variance*) versus log(*mean*)). Data were generally right-skewed and had a positive variance-mean relationship. The slope of the Taylor power plot was used to optimally decouple variance from mean by raising the data to the power of ((2-slope)/2) (McArdle et al., 1990). Consequently, species abundance data were ($x^{0.25}$) transformed, total abundance was transformed by log10(x+1), and a square root ($x^{0.5}$) transformation was applied to species richness. To examine broad-scale relationships between fish species and benthic habitat variables, we ran a canonical correlation analysis on the transect-level data matrix and then plotted the total structure coefficients of the fish in habitat space. The standardized redundancy output values of the model were used to measure the amount of variation for both fish species and benthic habitat variables.

To examine intermediate-scale relationships between fish species and benthic habitat variables, densities of fishes per patch types were examined. However, because all patch types were not equally available, we also standardized patch-use relative to habitat availability (patch selectivity) by subtracting proportional occurrence of each patch type from the proportional abundance for each species. Here, a positive association with a patch type revealed that more individuals were found in that patch type than would be expected given random habitat use (i.e., no selectivity). Conversely, a negative association revealed that fewer individuals were found in that patch type than would be expected by random habitat use. Finally, because microhabitat availability was not measured independently of fish presence, microhabitat use by fishes was restricted to graphical presentation.

Results

Seafloor composition

We sampled 11.15 linear km of seafloor within the 12× 10 km survey region, using submersible strip-transect methods. At broad-scales, benthic habitat variables were grouped *a posteriori* in order to reliably distinguish hard, mixed, and soft strata (Fig. 2). Hard stratum comprised patchy "high-relief outcrops" of rock, boulders, and sand. In contrast, mixed stratum comprised "low-relief outcrops" of cobbles and mud. Soft stratum comprised "homogeneous mud." The three broad-scale habitat strata also varied in their depth distribution, and strata and depth were strongly collinear. High-relief outcrops were generally shallower (60–100 m) than low-relief outcrops (90–150 m), and although homogeneous mud occurred in most depth ranges, it was the only stratum surveyed in deep offshore locations (80–260 m). Benthic habitat variables within each of the three strata were also strongly collinear. For example, rock always co-occurred with boulders and sand, forming complex high-relief outcrops in shallower water (i.e., <100 m). Therefore, if a species was correlated at broad spatial scales with high-relief outcrops, differentiating the relative importance of substratum composition, depth, or some corequisite would be problematic.

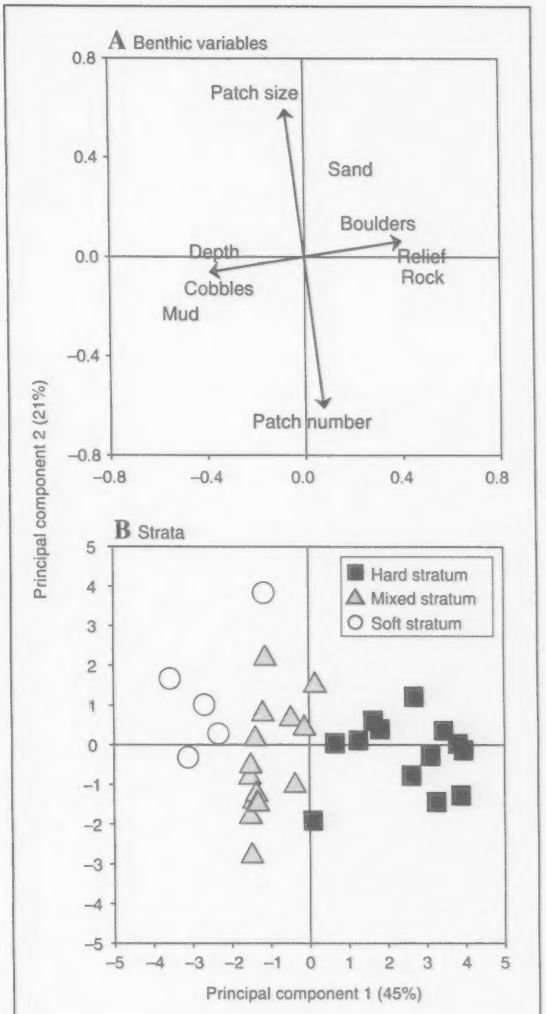


Figure 2

Principal components analysis of broad-scale benthic habitat characteristics: (**A**) correlation matrix of benthic variables; (**B**) projection of strata categories in ordination space.

Variability in intermediate-scale habitat also was discernible (Fig. 3). Five substrata (rock, boulders, cobbles, sand, and mud) were recorded during this survey, which at intermediate scales were present in 21 of 25 possible paired "substratum patch types" (all but mud-sand, cobble-sand, sand-cobble, or sand-mud patches types were recorded). However, the proportional availability of these patch types differed between strata. For example, hard strata contained the highest number

of substratum types (n=19), where rock and boulders types were the most abundant (Fig. 3A). Mixed strata also contained a variety of patch types (n=10), but were devoid of rock and contained higher proportions of mud (Fig. 3B). Soft strata contained the fewest patch types (n=3), composed primarily of homogeneous mud, and small amounts of homogeneous sand and mud-cobble patch types (Fig. 3C).

Structure of fish assemblages and broad-scale fish-habitat associations

Sixty-two species of demersal fishes (from 21 families) totalling 21,184 fishes were recorded during this survey. Rockfishes were the most abundant portion of the demersal fish assemblage, representing 93% of all fish sampled (i.e., 24 rockfish species, totalling 19,668 rockfishes). Most fishes recorded (96%) were small (TL ≤20 cm) noncommercial species, dominated by small-bodied (dwarf) rockfishes, such as *S. wilsoni* (n=5857, 28% of all fish sampled), *S. semicinctus* (halfbanded rockfish) (n=5247, 25%), and *S. hopkinsi* (squarespot rockfish) (n=2747, 13%). In comparison, both small (TL ≤20 cm) and large (TL >20 cm) fishes of commercial species and large noncommercial species were uncommon (462 small-size commercial fish (2%); 295 large-size commercial fish (1%); and 79 large-size noncommercial fish (0.4%)).

Fish density and species richness varied between the three broad-scale strata. Hard stratum had the highest density of fish (1357 fishes per 1000 m^2), followed by mixed stratum (862 fishes per 1000 m^2), and both strata were dominated by rockfishes (90%, 98% respectively). Inversely, soft stratum had comparatively few fish (130 fishes per 1000 m^2), dominated by nonrockfish species (63%). Small-size fishes accounted for the majority of demersal fishes within hard (98% of all fish sampled), mixed (99%), and soft (79%) strata. In comparison, large demersal fishes (TL>20 cm) were relatively uncommon in all three substrata; however, the hard stratum had higher densities (27 per 1000 m^2 [2% of all fishes in hard substratum]) than the soft (21 per 1000 m^2 [16%]), or mixed (4 per 1000 m^2 [0.5%]) strata. The mixed stratum had the highest number of species (44 species), where 64% of the species composition comprised nonrockfish species. The hard stratum had slightly fewer species (41 species) but comprised a more even mix of rockfish (54%) and nonrockfish (46%) species. Soft stratum had the fewest species of all three strata (19 species), of which most were nonrockfish species (74%). The number of commercially important species decreased as habitat complexity decreased: 18 commercial species (15 rockfish species) were recorded from hard substratum, compared with 16 (10 rockfish species) in mixed substratum, and 11 (5 rockfish species) in soft substratum.

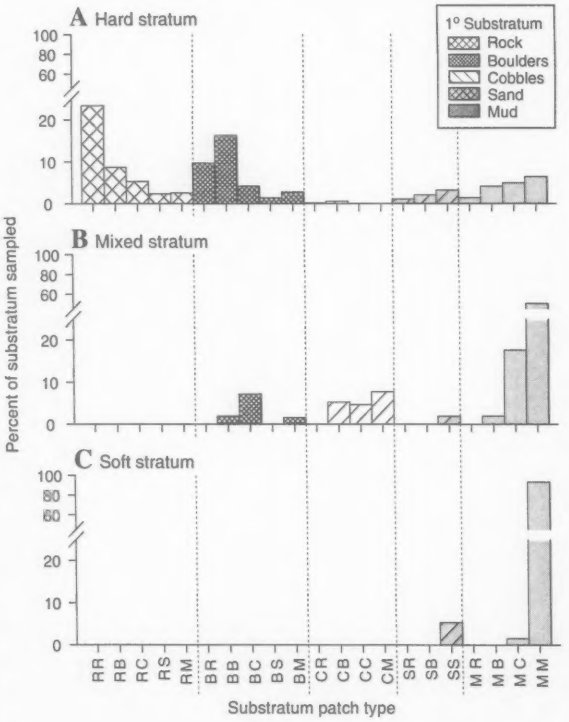


Figure 3

Intermediate-scale habitat characteristics: substratum patch composition within the three broad-scale habitat strata: (**A**) hard stratum, (**B**) mixed stratum, and (**C**) soft stratum. Substratum types recorded were R=rock, B=boulders, C=cobbles, S=sand, and M=mud. The first and second letters of each patch type (e.g., RR, RB, RC, to MM) represent primary (50%) and secondary (20%) substratum types, respectively.

Assemblage composition varied between the three broad-scale strata (Fig. 4). High-relief outcrops (hard stratum) were characterized by schools of small-bodied rockfishes (*S. hopkinsi*, *S. wilsoni*, and YOY), a suite of large-bodied rockfish (e.g., *S. paucispinis*, *S. flavidus*, *S. rubrivinctus* [flag rockfish], *S. rosaceus* [rosy rockfish], and *Sebastomus* spp.), and a few nonrockfish species (e.g., *R. nicholsii* and *O. elongatus*). Low-relief outcrops (mixed stratum), in contrast, were characterized by schools of the small-bodied rockfish, *S. semicinctus*, two large-bodied rockfishes (*S. chlorostictus* [greenspotted rockfish] and *S. elongatus* [greenstriped rockfish]), and a variety of nonrockfish species (e.g., *Citharichthys* spp., *Zalembius rosaceus* [pink seaperch], *Zaniolepis* spp. [combfishes], *Argentina sialis* [Pacific argentine], and *O. elongatus*). Homogeneous mud areas (soft stratum) differed from high-relief and low-relief outcrops

by the characteristic presence of Pleuronectiformes and Agonidae.

Intermediate- and fine-scale fish-habitat associations

At the level of the individual fish species, a range of benthic habitat variables and spatial scales were important in explaining species-specific distributions. Intermediate-scale information on patch use, patch selectivity, along with fine-scale microhabitat use, revealed four types of species-specific groups (Fig. 5–8).

The first group, rock and boulder associates (e.g., *S. hopkinsi*, *S. flavidus*, and *S. paucispinis*) were species that at the intermediate-scale were strongly associated with patches of rock or boulders (or both) (Fig. 5). At the fine-scale, these three species were found on or above rocks (69%, 76%, and 30%, respectively) or boulders (28%, 24%, and 18%, respectively); *S. paucispinis* also used mud microhabitats (52%).

The second group, generalists (e.g., *S. wilsoni*, *S. rosaceus*, and *O. elongatus*) were species that at the intermediate-scale were associated with a variety of patch types (Fig. 6). However, when standardized by habitat availability, these species were strongly associated with patches of boulders, cobbles, and to a lesser extent, rock, and were negatively associated with patches of homogeneous mud. At the fine-scale, these species were also found on or above all possible microhabitat types and showed a flexibility in habitat use at all three spatial scales. Ontogenetic shifts in habitat use also were indicated. For example, small *O. elongatus*, (<25 cm; n=54) were more abundant in patches with mud or cobbles (e.g., 74% in mud-mud [MM], cobble-boulder [CB], and mud-cobble [MC]), whereas medium-size *O. elongatus* (25–50 cm; n=57) were found more frequently in patches with boulders (40%) and rock (32%). Larger individuals (>50 cm; n=6), on the other hand, were found in patches of rock (83%), indicating that *O. elongatus* move from mixed mud and cobble habitats to more complex rocky outcrops as they grow.

The third group, cobble-mud associates (e.g., *S. semicinctus*, *S. chlorostictus*, and *S. elongatus*) were species that at the intermediate-scale were found in patches containing various mixtures of cobbles, mud, and to a lesser extent, boulders (Fig. 7). At the fine-scale, these species were found over mud (66%, 54%, and 81%, respectively) or low-relief cobbles and boulders (pooled 33%, 47%, and 16%, respectively) indicating that mud habitats adjacent to or within mixed cobble-mud areas had inherent properties above either habitat in isolation.

Finally, the fourth group, soft-sediment associates (e.g., Pleuronectiformes, Agonidae, *Citharichthys* spp., and *R. nicholsii*) were species that at the intermediate-scale were strongly associated with patches containing mud or sand (Fig. 8). Pleuronectiformes, Agonidae, and *Citharichthys* spp. were all associated with homogeneous soft sediments at all spatial scales (Fig. 8, A–C). In contrast, *R. nicholsii* were found in a range of soft-sediment patch types (e.g., sand-boulder [SB], sand-sand [SS], mud-rock [MR], mud-boulder [MB], etc.) and microhabitats. However, homogeneous soft-sediment areas had few or no *R. nicholsii* (Fig. 8D), indicating that, for this species, sediment gaps within a rocky outcrop matrix had inherent properties above either rock or sediment habitats in isolation.

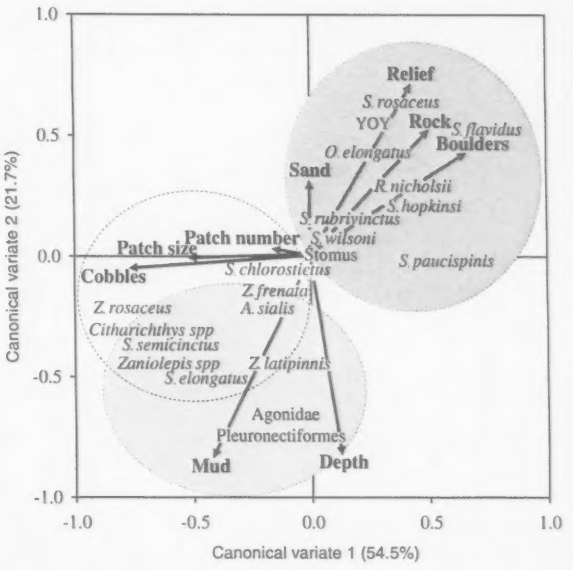


Figure 4

Broad-scale associations of the demersal fish assemblages with benthic habitat variables as discerned from canonical correlation analysis. Circles depict the three broad-scale strata (dark gray=hard, white=mixed, light gray=soft sediment), and are presented to assist in the visual association of species and benthic habitat variables. Vectors are the eigenvectors of the benthic habitat variables. YOY = young-of-year *Sebastes* spp., "Stomus" = *Sebastomus* spp.; *S = Sebastes; R = Rhinogobius; O = Ophiodon; Z = Zaniolepis; and A = Argentina.*

Discussion

The composition, complexity, and configuration of the seafloor at multiple scales allowed us to predict assemblage structure and species distributions across the continental shelf within southern Monterey Bay. Broad-scale habitat strata, which are routinely mapped by acoustic methods, showed clear distinctions in assemblage structure. Hard stratum, composed of high-relief outcrops, was occupied by a diverse range of demer-

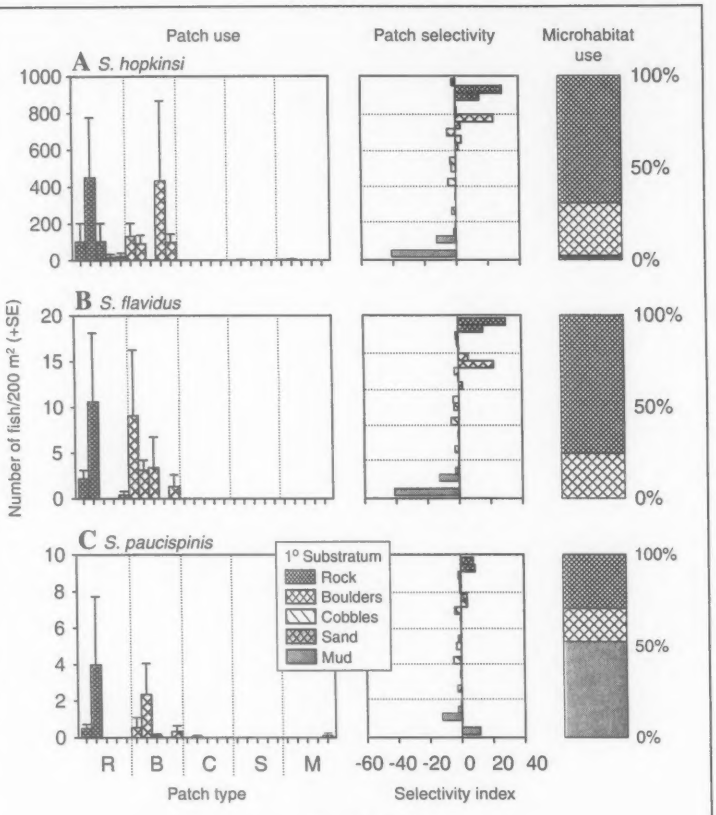


Figure 5

Intermediate and fine-scale habitat use by rock and boulder associates: (**A**) squarespot rockfish (*Sesbastes hopkinsi*) (**B**) yellowtail rockfish (*S. flavidus*), and (**C**) bocaccio (*S. paucispinis*). At the intermediate-scale, patch types (i.e., R=rock, B=boulders, C=cobbles, S=sand, and M=mud) are represented by primary (tick labels and shading) and secondary (sequence of ticks within each primary category R, B, C, S, and M) substratum categories and are ordered from hard (left=rock-rock [RR], rock-boulder [RB], rock-cobble [RC]...) to soft (right = ... mud-cobble [MC], mud-sand [MS], mud-mud [MM]) substratum types. "Patch use" depicts the mean number of fish plus standard errors (SE) found in each patch type. "Patch selectivity" depicts the relative patch use by fish, standardized by patch availability: graphs indicate positive (right-hand side of the plot) or negative (left-hand side of the plot) associations with patch types (ordered from hard (top=RR, RB, RC...) to soft (bottom= ... MC, MS, MM) substratum types) and the relative strengths of these associations. Fine-scale microhabitat use is represented by the proportion of fish found on or above a particular substratum type.

sal fish species dominated by small rockfish species. Although hard stratum was the least common of the three strata (Anderson et al., 2005), it supported the highest overall densities of fish, including more commercial species, than either mixed or soft strata. High fish densities, a dominance of small rockfish species, and the presence of large commercial species over high-relief outcrops have been recorded in other submersible surveys in California (Yoklavich et al., 2000, 2002), Oregon (Stein et al., 1992), Washington (Jagielo et al., 2003), British Columbia (e.g., Murie et al., 1994), and Alaska (O'Connell and Carlile, 1993). For example, Yoklavich et al. (2000) found high numbers of large commercially important rockfish species (e.g., *S. paucispinis*, *S. ruberrimus*, *S. levis* [cowcod]) associated with discrete rocky outcrops in a submarine canyon

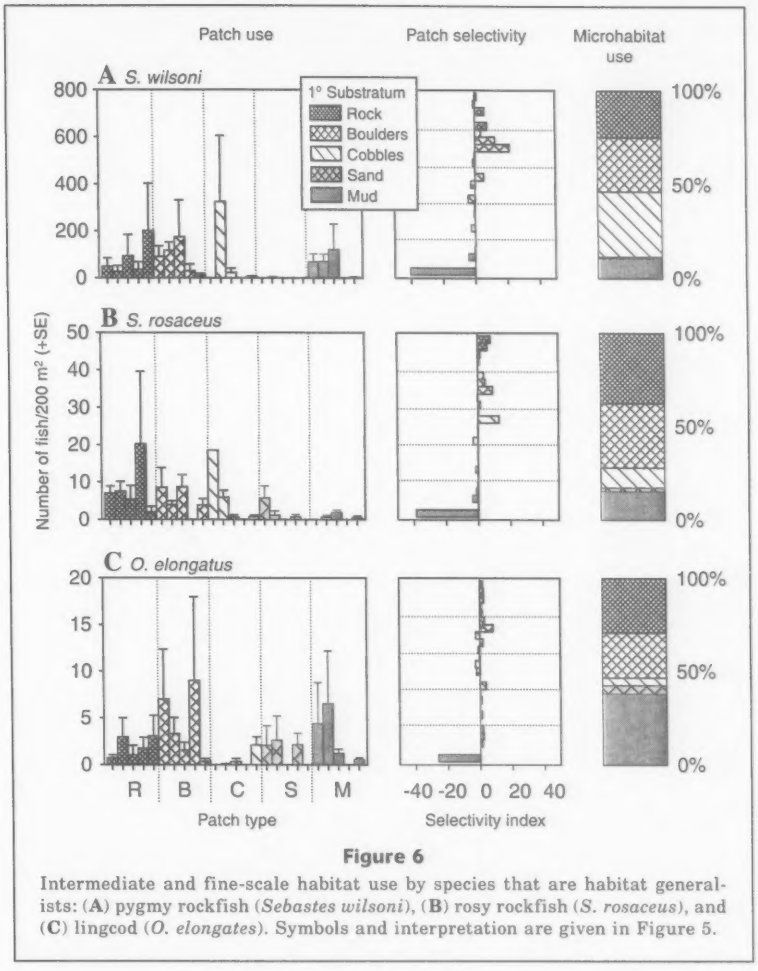


Figure 6

Intermediate and fine-scale habitat use by species that are habitat generalists: (**A**) pygmy rockfish (*Sebastes wilsoni*), (**B**) rosy rockfish (*S. rosaceus*), and (**C**) lingcod (*O. elongates*). Symbols and interpretation are given in Figure 5.

off central California. Jagielo et al. (2003) compared trawlable and untrawlable habitats off Washington and found rockfishes (*Sebastes helvomaculatus* [rosethorn rockfish], *S. rubberimus*, *S. flavidus*, *Sebastes nigrocinctus* [tiger rockfish], and *Sebastes* spp.) were three times more abundant in untrawlable habitats. In more complex habitat systems, Stein et al. (1992) found high densities of juvenile *Sebastes* spp. and *S. flavidus* on the tops of high-relief rocky pinnacles on Heceta Bank, Oregon, whereas in the Gulf of Alaska, O'Connell and Carlile (1993) found the commercially important *S. rubberimus* in highest densities in complex habitats.

Mixed stratum, characterized by lower complexity and relief than areas of hard stratum, also comprised a distinctive demersal fish assemblage with high numbers of species. High diversity in these areas resulted from a combination of species unique to the mixed stratum (e.g., *S. semicinctus*), and species characteristic of both hard (e.g., *S. wilsoni*, *O. elongatus*, *S. rosaceus*) and soft (e.g., Pleuronectiformes and Agonidae) strata. In addition to high diversity, some species (e.g., *S. chlorostictus*, *S. elongatus*, and *Z. frenata*) were also more abundant in the mixed stratum, indicating that some inherent property of heterogeneous habitats (e.g., multiple resource needs, higher levels of habitat fragmentation, and interface zones) may be important to these species. Similar findings have been reported in other submersible surveys. Stein et al. (1992), for example, found more species and higher densities of these species (e.g., *S. chlorostictus*, *S. wilsoni*) in patches with either "mud and boulder" or "mud and cobble" than in patches with mud, boulders, or cobbles in isolation. Species use of interface regions can also be inferred from previous studies even though habitat use at the microscale was not explicitly measured. For example, both Richards (1986) and Pearcy et al. (1989) reported higher numbers of *S. elongatus* in soft sediment areas adjacent to rocks. Similarly, Yoklavich et al. (2002) found that

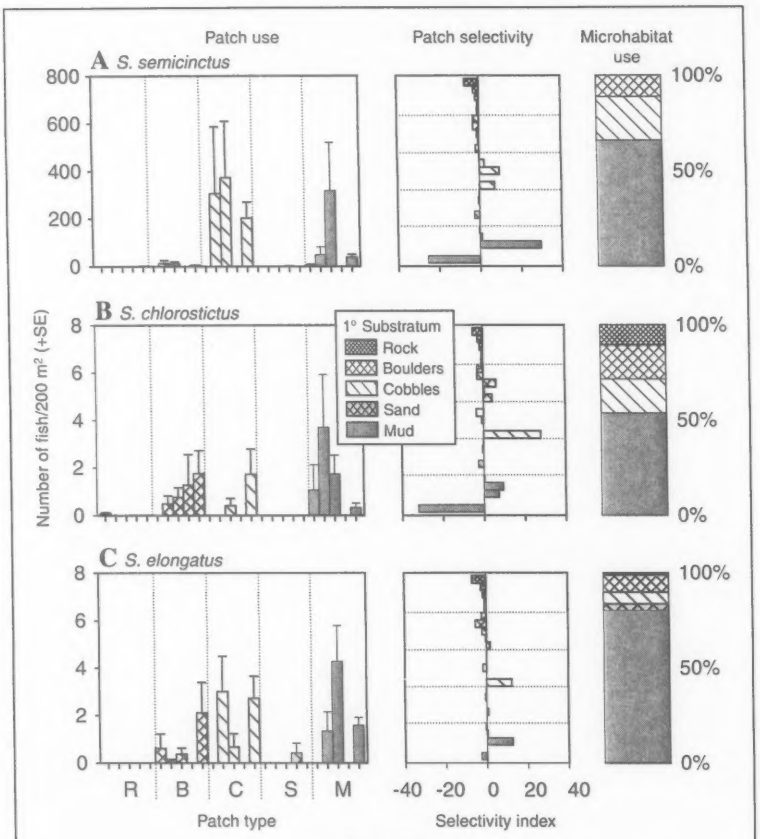


Figure 7

Intermediate and fine-scale habitat use by cobble-mud associates: (**A**) halfbanded rockfish (*Sebastes semicinctus*), (**B**) greenspotted rockfish (*S. chlorostictus*), and (**C**) greenstriped rockfish (*S. elongates*). Symbols and interpretation are given in Figure 5.

S. chlorostictus, along with other species, used habitats comprising a combination of rock and mud.

Soft substratum had the lowest habitat complexity and the lowest diversity and density of fishes of all three strata, although many of these species, particularly the Pleuronectiformes, are important commercial species. Stein et al. (1992), Yoklavich et al. (2000, 2002), and Jagielo et al. (2003) also recorded similar demersal fish assemblages in flat mud habitats (i.e., Pleuronectidae, namely *M. pacificus*, *Glyptocephalus zachirus* [rex sole], and *Lyopsetta exilis* [slender sole]), Agonidae, *Sebastes saxicola* [stripetail rockfish], Zoarcidae [eelpouts], and *Sebastolobus* spp. [thornyhead species]). Although demersal fish assemblages over trawlable habitats have been well documented by traditional fishery methods (e.g., Weinberg et al., 2002), biases in catchability between strata (because trawls may snag in complex habitats) mean that differences in fish assemblage structure between soft, mixed, and hard strata have been difficult to identify. Although *in situ* submersible surveys facilitate these types of comparisons, some biases may still be present. For example, soft-sediment habitats reported in submersible studies (e.g., Stein et al., 1992; O'Connell and Carlile, 1993; Yoklavich et al., 2002) are often adjacent to, at the base of, or in the general vicinity of rock outcrops. As a result, it is unclear how the proximity of hard structure influences demersal fish composition and abundance, or whether these habitats are representative of soft-sediment areas where rock outcrops are not present. The analysis of submersible transects in relation to distance from rocks, or alternatively trawl surveys that include video or acoustic images of the benthos, may help to clarify these patterns.

All three spatial scales provided valuable information on how demersal fish species use benthic habitats.

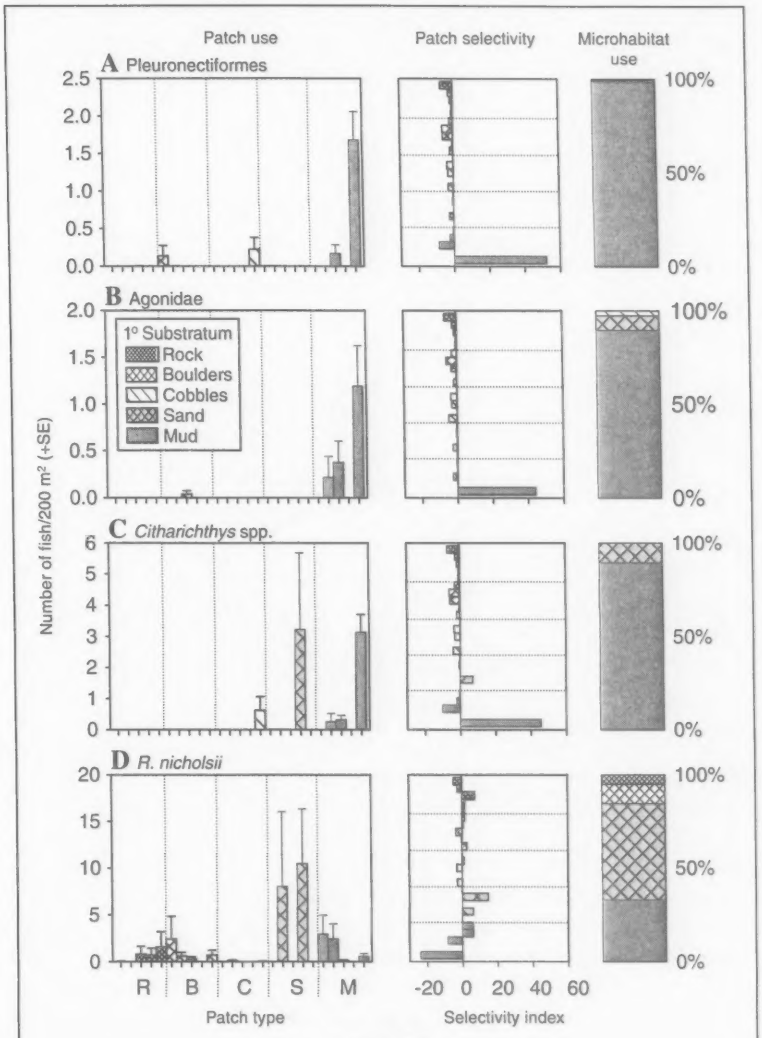


Figure 8

Intermediate and fine-scale habitat use by soft-sediment associates: (**A**) flatfishes, Pleuronectiformes, (**B**) poachers, Agonidae, (**C**) sanddabs, *Citharichthys* spp., and the blackeyed goby (*Rhinogobiops nicholsii*). Symbols and interpretation are given in Figure 5.

For example, broad-scale strata supported characteristic fish assemblages. However, at intermediate scales (within a strata), species distribution varied by patch composition, patch size, and the neighborhood of surrounding patches. At fine scales, microhabitat use by fishes indicated which portions of habitat-patches were actually used (e.g., species A in cobbles and species B in mud, where both species were present within the same cobble-mud patch). A vital aspect of using a multiscaled approach, however, was that information from each spatial scale could then be integrated to examine the relative importance of habitat types and their structural configuration, and this information also indicated that for some species the landscape context was important. For example, *R. nicholsii* was mainly found on sand or at the interface between sand and rock (microhabitat use), but these microhabitats were located within a range of rock and sediment patch types (intermediate-scale), which in turn were located within the complex hard stratum (broad-scale). This structure indicated

that for *R. nicholsii* sediment gaps within or adjacent to a rocky landscape were required.

On the other hand, *S. chlorostictus* and *S. elongatus* were both more abundant in the mixed stratum than in the hard stratum (broad scale) and were present together within mixed boulder, cobble, and mud substrata (intermediate scale). At fine scales, however, microhabitat use by these species differed; *S. elongatus* was common in the mud portion of these patches and *S. chlorostictus* was common over boulders and cobbles. These findings indicated that both species were interface associates, but within these interface regions different substratum types were used. The inclusion of microhabitat information within this multiscale approach provided a more comprehensive understanding of how demersal fish use benthic substrata. However, recording microhabitat use for each fish (n=21,184 fishes) was time consuming and therefore would likely negate its use in some studies. A recommended alternative method for recording microhabitat use might be to measure microhabitat use for a subset of fish per species, where subsamples are selected unbiasedly from the overall sample pool.

The ability to describe and predict fish-habitat relationships, as identified in this study, can be used to address area-based management concerns in several ways. For example, species captured by benthic trawl and long-line gear could be used to infer the presence of seafloor substratum types. Although this form of information is not novel, our study provides detailed quantitative species-habitat associations that validate this approach. For example, a benthic trawl that captures Pleuronectidae, Agonidae, *S. semicinctus*, *S. chlorostictus*, and *S. elongatus*, would indicate that the area trawled encompassed multiple strata (e.g., one or more areas of low-relief outcrop and homogenous mud). However, the proportions and spatial configuration of these strata would not be known unless a video camera, for example, was mounted on a benthic trawl (e.g., Abookire and Rose, 2005), or a seafloor substrata map was available for the area (e.g., Bellman et al., 2005).

Conversely, habitat could be used to predict community structure and species distributions. In this study, substratum type was a good indicator of distribution and abundance of many commercial and noncommercial fish species. However, the spatial arrangement and degree of habitat patchiness, in addition to substratum type, also were important predictive variables. Consequently, although areal estimates of substrata are likely to be effective for modeling the abundance and distribution of certain species (e.g., *S. rosaceus* and *S. flavidus*), accurately estimating other species will require additional knowledge of the spatial arrangement of these substrata. For example, species associated with sediment-rock interfaces, such as *S. chlorostictus*, *S. elongatus*, and *Z. frenata*, are likely to be modeled more effectively by estimating the perimeter of either an outcrop or specific habitat type. Likewise, the ability to model gap-associate species, such as *R. nicholsii*, will require information on the availability of sediment-outcrop interfaces and sediment gaps within an outcrop matrix. For other species, such as young-of-year rockfish, a measure of habitat patchiness, in combination with areal estimates of substrata, may be required. The ability to map this level of habitat detail will depend to a large degree on a trade-off between data acquisition and resolution of the mapping tools used, and the amount of seafloor needed to be mapped (Anderson et al., 2005).

In conclusion, the overall success of area-based management strategies will reflect the ability of researchers to accurately measure the functional relationships between organisms and their habitat. Multiscale *in situ* surveys, such as this one, undertaken in multiple locations, in combination with larger-scale fishery surveys can improve our understanding of the role of benthic habitats in structuring demersal fishes across the broader U. S. West Coast. These insights, in turn, improve our ability to characterize and map essential fish habitat, estimate habitat availability, and predict multispecies distributions and habitat associations within specified areas such as marine protected areas. Importantly, this study also provides a quantitative baseline of demersal fish assemblage structure for both commercial and noncommercial species, which is critical for future comparisons of spatiotemporal abundance, diversity, and habitat use. This baseline is also vital for assessing the effects and value of increased protection of West Coast shelf ecosystems.

Acknowledgments

We thank G. Cailliet, R. Lea, M. Love, G. Moreno, R. Parrish, P. Reilly, L. Snook, R. Starr, D. Sullivan, the *Delta* Oceanographics (R. Slater, D. Slater, and C. Ijames) for logistical support and biological data collection. We thank M. Carr, C. Grimes, S. Ralston, C. Syms, B. Tissot, and W. Wakefield for their conversations and advice during the analysis and writing of this research, and Tim Simmonds and Guy Cochrane for graphical support. The manuscript was improved through the comments of M. Cappo, C. Grimes, T. Laidig, C. Syms, and three anonymous reviewers. This project was partially supported by NOAA's National Undersea Research Program, West Coast and Polar Undersea Research Center, University of Alaska, Fairbanks (Grants UAF-92-0063 and UAF-93-0036) and by a University of California, Santa Cruz postdoctoral fellowship to Tara Anderson, with joint funding from National Marine Fisheries Service, U. S. Geological Survey, and the National Marine Protected Areas Center Science Institute.

Literature cited

Abookire, A. A., and C. S. Rose.
2005. Modifications to a plumb staff beam trawl for sampling uneven, complex habitats. Fish. Res. 71: 247–254.

Adams, P. B., J. L. Butler, C. H. Baxter, T. E. Laidig, K. A. Dahlin, and W. W. Wakefield.
1995. Population estimates of Pacific coast groundfishes from video transects and swept-area trawls. Fish. Bull. 93:446–455.

Addicott, J. F., J. M. Aho, M. F. Antoun, D. K. Padilla, J. S. Richardson, and D. A. Soluk.
1987. Ecological neighbourhoods: scaling environmental patterns. Oikos 49:340–346.

Anderson, T. J., M. M. Yoklavich, and S. L. Eittreim.
2005. Linking fine-scale groundfish distributions with large-scale seafloor maps: Issues and challenges of combining biological and geological data. *In* Benthic habitats and the effects of fishing (P. W. Barnes, and J. P. Thomas, eds.), p. 667–678. Am. Fish. Soc. Symp. 41, Bethesda, MD.

Ault, T. R., and C. R. Johnson.
1998. Spatially and temporally predictable fish communities on coral reefs. Ecol. Monogr. 68:25–50.

Bellman, M. A., S. A. Heppell, and C. Goldfinger.
2005. Evaluation of a US west coast groundfish habitat conservation regulation via analysis of spatial and temporal patterns of trawl fishing effort. Can. J. Fish. Aquat. Sci. 62:2886–2900.

Eittreim, S. L., R. J. Anima, and A. J. Stevenson.
2002. Seafloor geology of the Monterey Bay area continental shelf. Mar. Geol. 181:3–34.

Forman, R. T. T.
1995. Land mosaics: the ecology of landscapes and regions, 632 p. Cambridge Univ. Press, Cambridge, U.K.

Gunderson, D. R., and T. M. Sample.
1980. Distribution and abundance of rockfish off Washington, Oregon, and California during 1977. Mar. Fish. Rev. 42:2–16.

Jagielo, T., A. Hoffmann, J. Tagart, and M. Zimmermann.
2003. Demersal groundfish densities in trawlable and untrawlable habitats off Washington: implications for the estimation of habitat bias in trawl surveys. Fish. Bull. 101:545–565.

Jones, G. P., and C. Syms.
1998. Disturbance, habitat structure and the ecology of fishes on coral reefs. Aust. J. Ecol. 23:287–297.

Langton, R. W., P. J. Auster, and D. C. Schneider.
1995. A spatial and temporal perspective on research and management of groundfish in the Northwest Atlantic. Rev. Fish Sci. 3:201–29.

Love, M. S.
2006. Subsistence, commercial, and recreational fisheries. *In* The ecology of marine fishes: California and adjacent waters (L. G. Allen, D. J. Pondella, and M. H. Horn, eds.), p. 567–594. Univ. California Press, Berkeley, CA.

Love, M. S., and M. Yoklavich.
2006. Deep rock habitats. *In* The ecology of marine fishes: California and adjacent waters (L. G. Allen, D. J. Pondella, and M. H. Horn, eds.), p. 411–427. Univ. California Press, Berkeley, CA.

Love, M. S., M. Yoklavich, and L. Thorsteinson.
2002. The rockfishes of the northeast Pacific, 405 p. Univ. California Press, Berkeley and Los Angeles, CA.

McArdle, B. H., K. J. Gaston, and J. H. Lawton
1990. Variation in the size of animal populations: patterns, problems and artifacts. J. Anim. Ecol. 59: 439–454.

Murie, D. J., D. C. Parkyn, B. G. Clapp, and G. G. Krause.
1994. Observations on the distribution and activities of rockfish, *Sebastes* spp., in Saanich Inlet, British Columbia, from the *Pisces IV* submersible. Fish. Bull. 92:313–323.

O'Connell, V. M., and D. W. Carlile.
1993. Habitat-specific density of adult yelloweye rockfish *Sebastes ruberrimus* in the eastern Gulf of Alaska. Fish. Bull. 91:304–309.

Pearcy, W. G., D. L. Stein, M. A. Hixon, E. K. Pikitch, W. H. Barss, and R. M. Starr.
1989. Submersible observations of deep-reef fishes of Heceta Bank, Oregon. Fish. Bull. 87:955–965.

Richards, L. J.
1986. Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible PISCES IV. Environ. Biol. Fishes 17:13–21.

Stein, D. L., B. N. Tissot, M. A. Hixon, and W. H. Barss.
1992. Fish-habitat associations on a deep reef at the edge of the Oregon continental shelf. Fish. Bull. 90:540–551.

Stephens, J. S. Jr., R. J. Larson, and D. J. I. Podella.
2006. Rocky reefs and kelp beds. *In* The ecology of marine fishes: California and adjacent waters (L. G. Allen, D. J. Pondella, and M. H. Horn, eds.), p. 227–252. Univ. California Press, Berkeley, CA.

Syms, C., and G. P. Jones.
1999. Scale of disturbance and the structure of a temperate fish guild. Ecology 80:921–940

Weinberg, K. L.
1994. Rockfish assemblages of the middle shelf and upper slope off Oregon and Washington. Fish. Bull. 92:620–632.

Weinberg, K. L., M. E. Wilkins, F. R. Shaw, and M. Zimmermann.
2002. The 2001 Pacific west coast bottom trawl survey of groundfish resources: estimates of distribution, abundance, and length and age composition. NOAA Tech. Memo. NMFS-AFSC-128, 140 p.

Wiens, J. A.
1989. Spatial scaling in ecology. Funct. Ecol. 3:385–397.

Williams, E. H., and S. Ralston.
2002. Distribution and co-occurrence of rockfishes (family: Sebastidae) over trawlable shelf and slope habitats of California and southern Oregon. Fish. Bull. 100:836–855.

Yoklavich, M. M., G. M. Cailliet, R. N. Lea, H. G. Greene, R. M. Starr, J. de Marignac, and J. Field.
2002. Deepwater habitat and fish resources associated with the Big Creek Marine Ecological Reserve. CalCOFI Rep. 43:120–140.

Yoklavich, M. M., H. G. Greene, G. M. Cailliet, D. E. Sullivan, R. N. Lea, and M. S. Love.
2000. Habitat association of deep-water rockfishes in a submarine canyon: an example of a natural refuge. Fish. Bull. 98:625–641.

Use of endoparasitic helminths as tags in delineating stocks of American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence and Cape Breton Shelf

Gary McClelland (contact author)

Jason Melendy

Fisheries and Oceans Canada
Gulf Fisheries Centre
343 University Avenue
Moncton, New Brunswick
E1C 9B6 Canada

Email address for G. McClelland: mcclellandg@dfo-mpo.gc.ca

Abstract—Endoparasitic helminths were inventoried in 483 American plaice (*Hippoglossoides platessoides*) collected from the southern Gulf of St. Lawrence, NAFO (North Atlantic Fisheries Organization) division 4T, and Cape Breton Shelf (NAFO subdivision 4Vn) in September 2004 and May 2003, respectively. Forward stepwise discriminant function analysis (DFA) of the 4T samples indicated that abundances of the acanthocephalans *Echinorhynchus gadi* and *Corynosoma strumosum* were significant in the classification of plaice to western or eastern 4T. Cross validation yielded a correct classification rate of 79% overall, thereby supporting the findings of earlier mark-recapture studies which have indicated that 4T plaice comprise two discrete stocks: a western and an eastern stock. Further analyses including 4Vn samples, however, indicated that endoparasitic helminths may have little value as tags in the classification of plaice overwintering in Laurentian Channel waters of the Cabot Strait and Cape Breton Shelf, where mixing of 4T and 4Vn fish may occur.

Manuscript submitted 17 May 2006 to the Scientific Editor's Office.

Manuscript approved for publication 25 August 2006 by the Scientific Editor.

Fish. Bull. 105:180–188 (2007).

American plaice (*Hippoglossoides platessoides*) are found in Northwest Atlantic waters along the continental shelf and upper continental slope from west Greenland to Rhode Island, favoring intermediate depths (90–250 m), cold waters (<0–1.5°C), and fine sand or mud bottom (Scott and Scott, 1988). Amercian plaice has ranked second in importance to Atlantic cod (*Gadus morhua*) among groundfish landed in the southern Gulf of St. Lawrence (North Atlantic Fisheries Organization [NAFO] division 4T) over the past four decades, but commercial landings, which had ranged from 4907 to 11,780 t between 1965 and 1992 (Morin et al.[1]), fell to 401 t by 2004 (Fisheries and Oceans Canada[2]). Commercial and research survey data show that declines in abundance of southern Gulf plaice since 1991 have occurred primarily in western 4T between the Gaspé Peninsula and the Magdalen Islands (see Fig. 1), and abundances east of the Magdalens have remained stable. The eastern and western 4T stocks monitored in recent assessments are consistent with the meristically indistinguishable "Miscou-Magdalen" and "Cape Breton" groups which Powles (1965) delineated through mark-recapture experiments. Powles (1965) suggested that the meristic uniformity of these two groups may be a consequence of larval drift because mature fish from the respective groups seldom mix on their summer feeding grounds. More recently, Stott et al. (1992) found no evidence of population subdivision of Southern Gulf plaice in respect to allozyme variation and restriction fragment length polymorphisms in mitochondrial DNA.

As evident from commercial catch records and tag returns, 4T plaice, with the exception of some immature fish that remain in the shoals year round, migrate from summer feeding grounds on the Magdalen Shallows to deeper waters of the Laurentian Channel in winter (Powles, 1965). The winter distribution of plaice in the Laurentian Channel is continuous from the Gaspé to the Cabot Strait (Clay, 1991) and eastward along the Cape Breton Shelf (NAFO subdivision

[1] Morin, R., I. Forest, and G. Poirier. 2001. Status of NAFO Division 4T American plaice, February 2001. Canadian Science Advisory Secretariat Research Document. 2001/023, 70 p. Fisheries and Oceans Canada, Science Branch, Marine Fish Division, Gulf Region, P.O. Box 5030, Moncton, New Brunswick, Canada.

[2] Fisheries and Oceans Canada. 2005. American plaice in the southern Gulf of St. Lawrence (Division 4T). Fisheries and Oceans Canadian Science Advisory Secretariat Science. Advisory Report. 2005/008, 5 p. Maritime Provinces, Regional Advisory Process, Fisheries and Oceans Canada, P.O. Box 1006, Dartmouth, Nova Scotia, Canada.

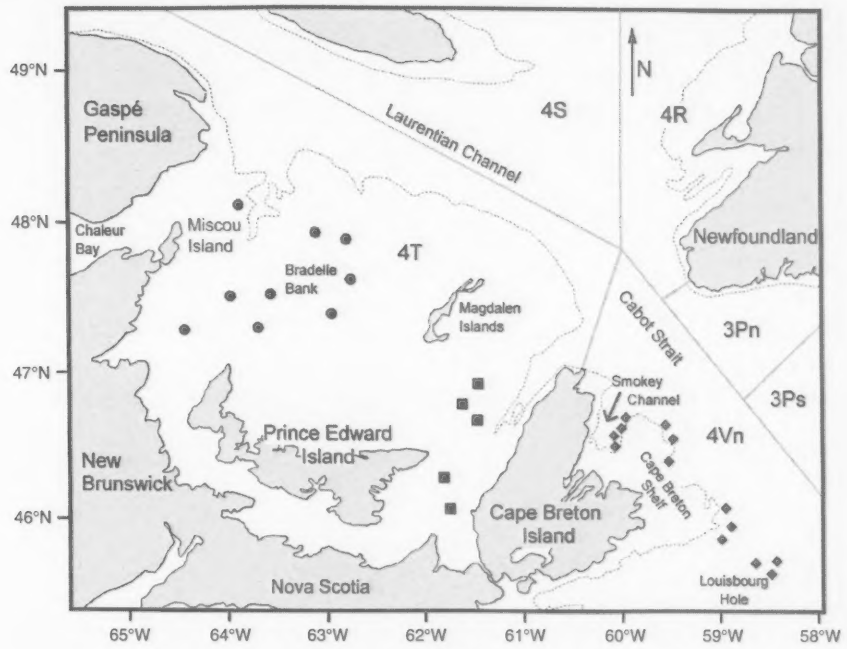


Figure 1

Map of eastern Canada indicating sites where American plaice (*Hippoglossoides platessoides*) were sampled in the southwestern (●) and southeastern (■) Gulf of St. Lawrence, and on or near the Cape Breton Shelf (♦). The depth contour (.....) is at 100 m. The pale gray lines demarcate North Atlantic Fisheries Organization divisions (4T, 4S. 4R) and subdivisions (3Pn, 3Ps, and 4Vn).

4Vn) (Swain et al., 1998). Clay (1991), noting the abundance of plaice in the Gulf portion of the Channel in January, surmised that southern Gulf plaice, unlike 4T cod, with which they are often closely associated, do not migrate through the Cabot Strait to over-winter in 4Vn. Length-at-age data from commercial landings indicate that plaice taken near the Cabot Strait late in the year are primarily from the slower growing eastern 4T (Cape Breton) stock (Tallman, 1991). A few older plaice tagged on Bradelle Bank, northwest of the Magdalen Islands, however, have been recovered in the Cabot Strait area in fall and winter (Powles, 1965). Clearly, tagging data and information on seasonal distributions from research surveys and commercial fisheries have provided little insight into the movements of 4T plaice stocks in the Laurentian Channel in winter and have not dispelled the possibility that 4T stocks may be exploited during the winter fishery within 4Vn.

Parasites as biological tags have often proven advantageous over more costly mark-recapture methods in studies of fish stock structure and migration (Williams et al., 1992) and are useful as markers in surveys for allocating quotas and combating illegal landings (Power et al., 2005). Parasite markers have shown potential in stock delineation of numerous demersal fish species (Marcogliese et al., 2003; MacKenzie and Abuanza, 2005; Melendy et al., 2005), including flatfish species such as Greenland halibut (*Reinhardtius hippoglossoides*) (Arthur and Albert, 1993; Boje et al., 1997), Pacific halibut (*Hippoglossus stenolepis*) (Blaylock et al., 2003), and winter flounder (*Pleuronectes americanus*) (McClelland et al., 2005). Although there have been no prior attempts to use parasite assemblages in describing the stock structure of American plaice, parasitological surveys of plaice in the Northwest Atlantic have identified a number of potential parasite tags. Scott (1975), for example, concluded that the enteric digeneans *Steringotrema ovacutum*, *Zoogonoides viviparous*, and *Fellodistomum furcigerum* might prove useful as tags for plaice stocks from the southern Gulf of St. Lawrence, Scotian Shelf, and northeastern Gulf of Maine. Zubchenko (1985) remarked that species compositions and infection parameters of 20 protozoan and metazoan parasites of plaice from the Grand Bank, Flemish Cap, and northeastern Newfoundland and Labrador are peculiar to their geographic origin. Finally, studies of the temporal and geographic distributions of larval sealworm (*Pseudoterranova decipiens*) (Nematoda) in Atlantic Canadian groundfish have revealed significant disparities in prevalence and abundance of sealworm in neighboring plaice stocks (McClelland et al., 2000; McClelland and Martell, 2001b).

The primary objective of the present study was to investigate the possibility of using parasite markers to delineate the western and eastern 4T plaice stocks, evident in earlier mark-recapture experiments (Powles, 1965). In light of potential mixing of southern Gulf and Cape Breton Shelf plaice over-wintering in the Laurentian Channel, parasite tags were also employed in an effort to examine the discreteness of 4T and 4Vn stocks.

Materials and methods

Sampling of the host

American plaice, 31 to 40 cm in total length, were collected from two locations in the southern Gulf of St. Lawrence (NAFO division 4T) and from three locations on or near the Cape Breton Shelf (NAFO subdivision 4Vn) (Fig. 1). Samples from the southern Gulf were collected from the Canadian Coast Guard Ship (CCGS) *Alfred Needler* and the CCGS *Teleost* during a Fisheries and Oceans Canada (DFO) demersal fish survey in September of 2004, and plaice from the Cape Breton Shelf were sampled from the *Alfred Needler* in May 2003 during a dedicated survey of parasites and diseases in 4Vn groundfish. Fish were caught with a Western IIA otter trawl which was towed for 30 minutes at each station. A total of 483 plaice were collected, including 137 plaice taken at depths of 43 to 88 m in the western 4T division and 95 plaice sampled at depths of 49 to 70 m in eastern 4T division. In the 4Vn survey, 128 plaice were sampled from the eastern slope of the Smokey Channel, 46 along the eastern edge of the Cape Breton Shelf, and 77 in the Louisbourg Hole. "Channel," "Edge," and "Hole" samples were taken at depths ranging from 77 to 124 m, 72 to 158 m, and 77 to 135 m, respectively. Samples were frozen onboard in a walk-in freezer at –17°C and transferred on landing to a –20° C walk-in freezer at the Gulf Fisheries Centre (GFC), Moncton, New Brunswick, where they were stored for future examination.

Individual fish were thawed at room temperature and measured lengthwise to the nearest centimeter. External surfaces and gills were inspected by eye for signs of trauma and other disease conditions. Viscera were examined for endoparasitic helminths with a dissecting microscope, and fillets were removed and sliced into thin sections (McClelland and Martell, 2001a) for detection of larval digeneans and nematodes. All helminth parasites were counted with the exception of *Stephanostomum baccatum* metecercariae. Because the latter were often too numerous and too widely distributed in host tissues to be counted within a reasonable time frame, only their presence was noted.

Statistical analysis

Prevalence (P) and abundance (A) of individual parasite species were calculated according to the methods of Bush et al. (1997), with prevalence being the numbers of infected fish in a sample divided by the total number of fish in a sample, expressed as a percentage, and abundance being the total number of parasites recovered from a sample divided by the total number of fish in a sample. Individual fish were coded 1 (infected), or 0 (uninfected) (Li, 1964; Neter et al., 1985) for analyses of prevalence, and a log $(n+1)$ transformation was used to bring the distributions of parasite counts closer to normality (Sokal and Rohlf, 1969; Platt, 1975). Parasite infection parameters that best distinguished between sampling locations were selected by forward stepwise discriminant function analysis (DFA). The Kappa statistic (K) was used to determine the improvement over chance of DFA (Titus et al., 1984). Misclassification rates of DFAs were calculated by employing cross validation procedures described by Arthur and Albert (1993) and Boje et al. (1997). All statistical procedures were performed with Systat for windows, vers. 7.0 (SPSS Inc., Chicago, IL). Because the survey was confined to plaice in a narrow length range (31–40 cm TL) (McClelland et al., 2000), effects of host size on parasite infection parameters were not investigated. Plaice from the edge of the Cape Breton Shelf were not included in the DFA analysis because of the small sample size (n=46) and the fact that they were collected from two widely separated groups of trawl sets (Fig. 1); the northern (n=21) and southern (n=25) portions of the sample were more distant from each other than were the samples from Smokey Channel and Louisbourg Hole.

Results

Plaice sampled from the southern Gulf of St. Lawrence (NAFO Division 4T) and the Cape Breton Shelf and vicinity (NAFO subdivision 4Vn) ranged from 31 to 40 cm in total length (TL), but the great majority fell within the lower half of this range. Mean length of fish (±standard error) was 32.34 ±0.180 cm (n=137) for plaice from the western 4T sample, and 32.31 ±0.22 cm (n=95) for the eastern 4T sample. Mean lengths of 4Vn plaice were 33.17 ±0.26 cm (n=128) and 32.88 ±0.23 cm (n=77) for Smokey Channel and Louisbourg Hole fish, respectively.

Eleven species of endoparasitic helminths were identified during routine parasitological examinations of 483 plaice (Table 1), but the larval digeneans *Otodistomum* sp., plerocercoid larvae of an unknown cestode species, and the nematode *Hysterothylacium aduncum* were observed too infrequently (<4% prevalence in all samples) to be considered useful as biological tags (see MacKenzie and Abaunza, 1998). Forward stepwise DFA of infection parameters of the remaining species revealed that abundances of the acanthocephalans *Corynosoma strumosum* and *Echinorhynchus gadi* contributed significantly to the classification of plaice from the southwestern and southeastern Gulf of St. Lawrence (K=0.57) and that *E. gadi* abundance was the more significant variable (Table 2). Cross-validation yielded an overall rate of 79% correct classification (Table 3), and the lowest rate of misclassification (15%) was found in fish from the

western 4T division. Abundances of *C. strumosum* (F=9.58), the digenean *Fellodistomum* sp. (F=11.61), and the larval anisakine nematode *Pseudoterranova decipiens* (F=8.89), and prevalence of the larval digenean *Stephanostomum baccatum* (F=8.64) were significant factors in the classification of 4Vn plaice from Smokey Channel and Louisbourg Hole (K=0.40), and cross-validation resulted in an overall classification efficiency of 70% (Table 4).

Stepwise DFA of helminth infections in plaice from all four sampling locations indicated abundances of *E. gadi* (F=35.80), *C. strumosum* (F=13.89), *Fellodistomum* sp., (F=5.81), and *P. decipiens* (F=4.75) and the prevalence of *S. baccatum* (F=5.71) were significant markers (K=0.30) for the classification of plaice from the entire (4T–4Vn) survey area. The overall rate of correct classification, however, was only 48%, and 51% of the plaice from western 4T divison were misclassified as 4Vn fish (Table 5). In a final analysis of samples from the east and west coasts of Cape Breton Island (eastern 4T and Smokey Channel, respectively), *E. gadi* abundance was again the most important marker selected (F=59.10), although abundances of the larval anisakine nematodes *Anisakis simplex* (F=6.50) and *Contracaecum osculatum* (F=6.60) also contributed significantly to classification (K=0.49). Cross-validation yielded a 77% rate of overall correct classification, but, although nearly all Smokey Channel plaice were classified correctly, more than half of the plaice from eastern 4T were misclassified as Smokey Channel fish (Table 6).

Table 1

Prevalence (P) (%) and abundance (A) of parasitic helminths in American plaice (*Hippoglossoides platessoides*) sampled from the southwestern (Western 4T) and southeastern (Eastern 4T) Gulf of St. Lawrence, Smokey Channel, edge of the Cape Breton Shelf, and Louisbourg Hole in 4Vn. Parasite. n/a=not available.

	Location (n)									
	Western 4T (n=137)		Eastern 4T (n=95)		Smokey Channel (n=128)		Edge of shelf (n=46)		Louisbourg Hole (n=77)	
Species	P	A	P	A	P	A	P	A	P	A
Digenea										
Hemiuriformes										
Derogenes varicus	4	0.04 ±0.02	6	0.06 ±0.03	3	0.17 ±0.05	24	0.30 ±0.09	16	0.17 ±0.05
Otodistomum sp.[1]	0	0	0	0	1	0.01 ±0.01	2	0.02 ±0.02	0	0
Strigeiformes										
Fellodistomum sp.	29	0.89 ±0.17	26	1.3 ±0.38	45	2.6 ±0.51	19	1.3 ±0.93	17	0.46 ±0.19
Plagiorchiiformes										
Stephanostomum baccatum[1]	15	n/a	33	n/a	33	n/a	24	n/a	13	n/a
Cestoda										
Cestoidea										
Unidentified cestode [1]	3	0.03 ±0.01	1	0.02±0.02	3	0.11 ±0.09	0	0	4	0.04±0.02
Nematoda										
Ascaridida										
Anisakis simplex[1]	10	0.13 ±0.03	8	0.08 ±0.03	22	0.23 ±0.04	15	0.19 ±0.07	21	0.21±0.05
Hysterothylacium Aduncum	1	0.01 ±0.0007	4	0.04 ±0.02	2	0.02 ±0.01	0	0	3	0.04±0.03
Contracaecum osculatum[1]	26	0.64 ±0.18	15	0.31 ±0.1	39	0.74 ±0.17	9	0.11 ±0.06	34	0.66±0.17
Pseudoterranova decipiens[1]	73	1.5 ±0.12	67	1.34 ±0.13	68	1.77 ±0.18	60	1.4 ±0.32	50	0.97±0.15
Acanthocephala										
Palaeacanthocephala										
Echinorhynchus gadi	7	0.1 ±0.031	50	1.3 ±0.3	4	0.09 ±0.05	0	0	13	0.27±0.1
Corynosoma strumosum[1]	8	0.15 ±0.06	30	0.5 ±0.15	25	0.48 ±0.1	33	1.6 ±0.6	38	2.1±0.9

[1] Larval.

Discussion

Forward stepwise DFA of parasite tags has been successfully employed in describing the stock structure of various flatfish species. Arthur and Albert (1993) used five species of larval helminth to classify widely separated stocks of Greenland halibut from the Saguenay fiord, St. Lawrence estuary, Labrador coast, and Baffin Island, amd Boje et al. (1997) used six helminth species to gain insight into the stock structure of Greenland halibut from northeastern Newfoundland and Greenland. The overall correct classification rate was >99% in the former, and 77% in the latter study. Blaylock et al. (2003) used eight helminth species to describe the stock structure of Pacific halibut along the Pacific coast of North America from the Bering Sea to northern California and achieved an overall correct classification rate of 83%. In all three studies, accuracy of classification increased when the numbers of geographical categories were reduced by pooling sampling locations.

Table 2

Results of forward stepwise discriminant function analysis of samples of American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence (North Atlantic Fisheries Organization Division 4T) showing the relative importance of abundances of two species of acanthocephalan in the classification of individual fish to western and eastern 4T stocks.

Variable	Standardized coefficient of first canonical variable	df	*F* score	Eigenvalue
Echinorhynchus gadi	0.862	230	71.48	0.46
Corynosoma strumosum	0.499	229	20.84	

Table 3

Cross-validation of American plaice (*Hippoglossoides platessoides*) from the western and eastern North Atlantic Fisheries Organization division 4T (southern Gulf of St. Lawrence) determined by discriminant function analysis of abundances of two species of acanthocephalans.

Location	Western 4T	Eastern 4T	% Correct
Western 4T	117	20	85
Eastern 4T	28	67	71
Totals	145	87	79

Table 4

Cross-validation of American plaice (*Hippoglossoides platessoides*) from the Smokey Channel and Louisbourg Hole, North Atlantic Fisheries Organization subdivision 4Vn, as revealed by discriminant function analyses of the prevalence or abundance of four helminth species (prevalence of *Stephanostomum baccatum*, and abundances of *Fellodistomum* sp., *Corynosoma strumosum*, and *Pseudoterranova decipiens*).

Location	Smokey Channel	Louisbourg Hole	% Correct
Smokey Channel	86	42	67
Louisbourg Hole	20	57	74
Totals	105	99	70

Although our survey was confined to a much smaller geographic area than those surveyed in the studies above, the accuracy of classification of plaice stocks from the southern Gulf of St. Lawrence (NAFO division 4T) is remarkably high (79%) (Table 3). DFA with only two markers, namely the abundances of the acanthocephalans *E. gadi* and *C. strumosum*, indicated that southern Gulf plaice consist of discrete western and eastern stocks on their summer feeding grounds; this result supports the results of earlier mark-recapture studies (Powles, 1965). Because the acanthocephalans are acquired passively in prey, and 4T plaice feed primarily in the Magdalen Shoals, spring through fall, while fasting in winter (Swain et al., 1998), these markers may also be employed in studies of seasonal migrations and mixing of the two stocks. Analysis of infection parameters of four helminth taxa (abundances of *C. strumosum*, the digenean *Fellodistomum* sp., the larval anisakine nematode *Pseudoterranova decipiens*, and prevalence of the larval digenean *Stephanostomum baccatum*) reveals a somewhat lower degree of discreteness (70% correct classification) between plaice from Smokey Channel and Louisbourg Hole, within NAFO subdivision 4Vn .

Abundances of *Fellodistomum* sp., *P. decipiens*, *E. gadi*, and *C. strumosum*, and prevalence of *S. baccatum* are significant factors in a DFA of plaice from all four locations, although the overall accuracy of classification falls to only 48% (Table 5). Although an improvement over random classification (25%), this latter result offers little encouragement for the use of parasites tags in future investigations of movements and possible mixing of 4T and 4Vn plaice overwintering in Laurentian Channel waters of the 4Vn subdivisioin. DFA of eastern 4T and Smokey Channel (4Vn) samples similarly seems to indicate that helminth tags would have little value in studies of the winter composition of plaice stocks in the Cabot Strait area. In this analysis, with the use of *E. gadi* and the larval nematodes *Anisakis simplex* and *Contracaecum osculatum* as markers, 98% of the 4Vn plaice were classified correctly, but 52% of the plaice from southeastern 4T were misclassified as 4Vn fish. However, given the differences in infection parameters of *E. gadi* in eastern 4T (prevalence [P]=50%, abundance [A]=1.30) and Smokey Channel samples (P=4%,

Table 5

Cross-validation of American plaice (*Hippoglossoides platessoides*) from the western and eastern North Atlantic Fisheries Organization (NAFO) division 4T and from Smokey Channel and Louisbourg Hole in NAFO subdivision 4Vn, as revealed by discriminant function analyses of the prevalence or abundance of five species of parasitic helminth (prevalence of *Stephanostomum baccatum*, and abundances of *Fellodistomum* sp., *Corynosoma strumosum*, *Echinorhynchus gadi*, and *Pseudoterranova decipiens*).

Location	Western 4T	Eastern 4T	Smokey Channel	Louisbourg Hole	% Correct
Western 4T	57	10	37	33	42
Eastern 4T	14	48	15	18	51
Smokey Channel	28	5	64	31	50
Louisbourg Hole	18	8	11	40	52
Totals	117	71	127	122	48

A=0.09) (Table 1), this acanthocephalan may yet prove to be a useful marker for the detection of southeastern 4T migrants among plaice overwintering in Cabot Strait and 4Vn.

Parasites that contributed to the DFAs above meet MacKenzie's (1987) criteria for biological tags. None of the helminths are known to reproduce directly on or in plaice. Each of the markers is abundant in fish from at least one of the sampling areas, and there are significant geographical variations in the infection parameters of each species within the survey area. The third criterion, that the parasite must be long-lived in the host, is clearly met by five species of larval helminth that contribute significantly to classification. Metacercariae of *S. baccatum*, the larval anisakines *A. simplex*, *C. osculatum*, and *P. decipiens*, and cystacanths of *C. strumosum*, found variously in the body cavity and musculature, are believed to survive indefinitely in the fish host and have been used as markers in other studies of flatfish stock structure (Arthur and Albert, 1993; Boje et al.,1997; Blaylock et al., 2003).

Although the life spans of enteric helminths (*Fellodistomum* sp. and *E. gadi*, herein) in marine fish remain largely unknown, it is possible that species infecting cold-water hosts may persist for several months or even years (Margolis and Boyce, 1969)—sufficient time to meet MacKenzie's (1987) criterion for tag longevity. *Echinorhynchus gadi* infecting a relict population of Atlantic cod in Lake Mogil'noye, Russia, for example, recruit in the fall and die off in late summer and early fall of the following year (Kulachkova and Timofeyeva, 1993). Similarly, *E. lageniformis* survive for about a year in the intestines of starry flounder (*Platichthys stellatus*) in the coastal waters of Oregon (Olson and Pratt, 1971). In any event, parasites need not be long lived in order to be suitable as markers, and there are numerous precedents for use of enteric helminths as markers in studies of host stock structure (Williams et al., 1992). Khan and Tuck (1995) identified *E. gadi* as an important indicator of the discreteness of Newfoundland cod stocks, and Power et al. (2005) employed abundances of enteric digeneans in classifying bogue (*Boops boops*) (Sparidae), a demersal species from Spanish fisheries.

Table 6

Cross-validation of American plaice (*Hippoglossoides platessoides*) to eastern North Atlantic Fisheries Organization (NAFO) division 4T and Smokey Channel (NAFO subdivision 4Vn) as revealed by discriminant function analyses of the abundances of three helminth species (abundances of *Echinorhynchus gadi*, *Anisakis simplex*, and *Contracaecum osculatum*).

Location	Eastern 4T	Smokey Channel	% Correct
Eastern 4T	46	49	48
Smokey Channel	3	125	98
Totals	49	174	77

Abundances of passively transmitted parasites are ultimately a function of host feeding behavior. Hence, geographical differences in intermediate-host abundance and frequency in plaice diets would manifest themselves as disparities in infection parameters of passively transmitted helminths in 4T and 4Vn plaice stocks. Digeneans, which mature in the digestive tract of marine fish, are usually acquired through the consumption of invertebrates (crustaceans, molluscs, polychaetes, and echinoderms, among other taxa) which harbor encysted metacercariae (Rohde, 2005). Brittle stars (Ophiuroidea), which are frequently exploited by both 4Tand 4Vn plaice (Powles, 1965; Minet, 1975), are host to the metacercariae of *Fellodistomum* sp. (Koie, 1980), an important influence in our DFAs involving 4Vn plaice. Larval anisakine nematodes (*A. simplex*, *C. osculatum*, and *P. decipiens*), which proved significant in stock delineation herein, are acquired through predation on the parasite's invertebrate hosts, usually crustaceans (Rohde, 2005). Although the life cycle of *A. simplex* is largely pelagic, the larvae may be transmitted to de-

mersal fish, such as plaice, by diurnal vertical migrants (euphausiids, shrimp, etc.) which feed pelagically at night but are found near the seafloor by day (McClelland, 1990). Larval *P. decipiens* infections are acquired through consumption of various benthic invertebrates, including mysids, isopods, amphipods, decapods, and polychaetes (McClelland, 2002) The acanthocephalan *E. gadi*, which was the most significant species in the classification of 4T plaice stocks in this study, reach maturity in the intestines of dozens of species of marine fish in the North Atlantic and use gammaridean and caprellid amphipods and mysids as intermediate hosts (Marcogliese, 1994).

Among influences on digenean infection parameters in fish are the distributions and abundances of molluscan intermediate hosts, where the parasites perform one or more generations of asexual reproduction. Brittle stars, which transmit *Fellodistomum* metacercariae to plaice, become infected by feeding on cercariae which develop in bivalve mollusks (Koie, 1980). In contrast to the other helminths used as markers here, the digenean *S. baccatum*, an important component of DFAs involving 4Vn plaice, is transmitted actively, through penetration of the skin by cercariae (Wolfgang, 1955). Mollusks that host the asexual reproduction of *S. baccatum* to the cercarial stage are whelks, especially the common or waved whelk (*Buccinum undatum*), which is widely distributed and commercially exploited in eastern Canadian waters.

Infection parameters of larval helminths in 4T-4Vn plaice may also be influenced by temporal and spatial distributions of the final hosts. The digenean *S. baccatum* matures and reproduces in the intestines of large piscivorous fish such as sea raven (*Hemitripterus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) (Wolfgang, 1955), and the anisakine nematode *A. simplex* matures and reproduces in the stomachs of cetaceans (Rohde, 2005). Adults of the anisakines *Contracaecum osculatum* and *P. decipiens*, and the acanthocephalan *C. strumosum* occur, respectively, in stomachs and intestines of seals. Surveys of various demersals in waters off Nova Scotia, Canada (Marcogliese and McClelland, 1992; McClelland et al., 2000; McClelland and Martell, 2001a&b) revealed that infection parameters of *P. decipiens* and *Corynosoma wegeneri* increased with proximity to Sable Island, site of the largest grey seal (*Halichoerus grypus*) colony in the Northwest Atlantic.

Spatial disparities in prevalences and abundances of parasitic helminths in fish may also be traced to variation of physical parameters (temperature, salinity, depth, and bottom habitat) that influence distributions of the invertebrate precursor hosts (Williams and Jones, 1994). Our 4T plaice samples were collected at relatively uniform depths (43–88 m), and the substrates in both sampling areas ranged from sandy pelite to sandy gravel and had outcroppings of sandstone bedrock (see Loring and Nota[3]). The mean near-bottom temperature for sampling stations in eastern 4T was 1.62 (0.49–3.23)°C (n=5), but only 0.21 (−0.01–0.77)°C (n=9) for stations in western 4T. Near-bottom temperatures prevalent on the Magdalen Shoals are extremely low throughout the year (Swain et al., 1998), and small variations in temperature may have dramatic effects on the developmental and transmission rates of helminth parasites, as well as on the distributions and developmental rates of their poikilothermic intermediate hosts. Hence, the fact that acanthocephalan infections in southeastern Gulf plaice were much heavier than those found in plaice from the northwestern Magdalen Shoals may, to some extent, reflect the relative warmth of waters occupied in eastern 4T.

In summary, DFAs of abundances of the acanthocephalans *E. gadi* and *C. strumosum* support the findings of earlier mark-recapture studies (Powles, 1965), which indicate the presence of distinct northwestern (Miscou-Magdalen) and southeastern (Cape Breton) plaice stocks in the southern Gulf of St. Lawrence. Moreover, both parasite markers could be employed in future studies of migration and mixing of the two 4T stocks within 4T, and infection parameters of *E. gadi* alone may prove useful for detecting the presence of southeastern 4T migrants among stocks overwintering in Laurentian Channel waters of the Cabot Strait and 4Vn. The strength of our conclusions may be mitigated, however, by the fact that 4T and 4Vn plaice were sampled only during September and May, respectively, and samples from the two areas were taken more than a year apart. Hence, the possibility of seasonal or longer term variations in infection parameters of enteric helminths, e.g., *Fellodistomum* sp. and *E. gadi*, could not be investigated. Finally, given problems inherent in stepwise procedures (Power et al., 2005), statistical procedures employed in the present study, and in similar studies, could be improved upon. Power et al. (2005), for example, adopted an "all possible subsets" approach to selection of indicator parasites used in linear and quadratic discriminant analyses and in nonparametric classification of bogue landed at Spanish fishing ports. Efforts will be made to address these shortcomings in future surveys.

Acknowledgments

The authors are grateful to T. Hurlbut, Fisheries and Oceans Canada, Moncton, for supervising the collection of plaice samples during the 2004 groundfish cruise in the southern Gulf of St. Lawrence. We also thank R. Morin, Fisheries and Oceans Canada, Moncton, and four anonymous referees for their helpful comments and advice on earlier drafts of the manuscript.

[3] Loring, D. H., and J. G. Nota. 1973. Morphology and sediments of the Gulf of St. Lawrence. Fisheries Research Board of Canada Bulletin, 182, 147 p. 116 Lisgart Street, Ottawa, Canada, K1A 0H3.

Literature cited

Arthur, J. R., and E. Albert.
1993. Use of parasites for separating stocks of Greenland halibut (*Reinhardtius hippoglossoides*) in the Canadian northwest Atlantic. Can. J. Fish. Aquat. Sci. 50:2175–2181.

Blaylock, R. B., L. Margolis, and J. C. Holmes.
2003. The use of parasites in discriminating stocks of Pacific halibut (*Hippoglossus stenolepis*) in the northeast Pacific. Fish. Bull. 101:1–9.

Boje, J., F. Riget, and M. Køie.
1997. Helminth parasites as biological tags in population studies of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum)), in the northwest Atlantic. ICES J. Mar. Sci. 54:886–895.

Bush, A. O., K. D. Lafferty, J. M. Lotz, and A. W. Shostak.
1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. J. Parasitol. 83:575–583.

Clay, D.
1991. Seasonal distribution of demersal fish (Osteichthyes) and skates (Chondrichthyes) in the southeastern Gulf of St. Lawrence. *In* The Gulf of St. Lawrence: small ocean or big estuary? (J. C. Therriault, ed.), p. 241–259. Can. Spec. Pub. Fish. Aquat. Sci. 113.

Khan R. A., and C. Tuck.
1995. Parasites as indicators of stocks of Atlantic cod (*Gadus morhua*) off Newfoundland, Canada. Can. J. Fish. Aquat. Sci. 52:195–201.

Koie, M.
1980. On the morphology and life-history of *Steringotrema pagelli* (Van Beneden, 1871) Ohdner, 1911 and *Fellodistomum fellis* (Olsson, 1868) Nicoll, 1909 [syn. *S. ovacutum* (Lebour, 1908) Yamaguti, 1953] (Trematoda, Fellodistomidae). Ophelia 19:215–236.

Kulachkova, V. G., and T. A. Timofeyeva.
1993. The acanthocephalan *Echinorhynchus gadi* (Zoega) from relict cod of Lake Mogil'noye. Can. Transl. Fish. Aquat. Sci. no. 5602.

Li, J. C. R.
1964. Statistical inference. Vol. 1, 658 p. Edwards Bros., Ann Arbor, MI.

MacKenzie, K.
1987. Parasites as indicators of host populations. Int. J. Parasit. 17:345–352.

MacKenzie, K., and P. Abaunza.
1998. Parasites as biological tags for stock discrimination of marine fish: a guide to procedures and methods. Fish. Res. 38:45–56.
2005. Parasites as biological tags. *In* Stock identification methods. Applications in fisheries science. (S. X. Cadrin, K. D. Friedland, and J. R. Waldman, eds.), p. 211–226. Elsevier Academic Press, San Diego, CA.

Marcogliese, D. J.
1994. *Aeginina longocornis* (Amphipoda: Caprellidea), new intermediate host for *Echinorhynchus gadi* (Acanthocephala: Echinorhynchidae). J. Parasitol. 80:1043–1045.

Marcogliese, D. J., E. Albert, P. Gagnon, and J. M. Sévigny.
2003. Use of parasites in stock identification of the deepwater redfish (*Sebastes mentella*) in the Northwest Atlantic. Fish. Bull. 101:183–188.

Marcogliese, D. J., and G. McClelland.
1992. *Corynosoma wegeneri* (Acanthocephala: Polymorphida) and *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) larvae in Scotian Shelf groundfish. Can. J. Fish. Aquat. Sci. 49:2062–2069.

Margolis, L., and N. P. Boyce.
1969. Life span, maturation and growth of two hemiurid trematodes, *Turbulovesicula lindbergi* and *Lecithaster gibbosus*, in Pacific salmon (Genus *Oncorhynchus*). J. Fish. Res. Board Can. 26:893–907.

McClelland, G.
1990. Larval anisakine nematodes in various fish species from Sable Island Bank and vicinity. *In* Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts (W. D. Bowen, ed.), p. 83–118. Can. Bull. Fish. Aquat. Sci. 222.
2002. The trouble with sealworms (*Pseudoterranova decipiens*, species complex, Nematoda): a review. Parasitol. 124(suppl.):183–203.

McClelland, G., and D. J. Martell.
2001a. Surveys of larval seal-worm, *Pseudoterranova decipiens* infection in various fish species sampled from Nova Scotian waters between 1988 and 1996, with an assessment of examination procedures. *In* Sealworms in the North Atlantic: ecology and population dynamics (G. Desportes, and G. McClelland, eds.), p. 57–76. North Atlantic Marine Mammal Commission Scientific Publications, Tromsø, Norway.
2001b. Spatial and temporal distributions of larval sealworm, *Pseudoterranova decipiens* (Nematoda: Anisakinae) in *Hippoglossoides platessoides* (Pleuronectidae) in the Canadian Maritime Region from 1993 to 1999. *In* Sealworms in the North Atlantic: ecology and population dynamics (G. Desportes, and G. McClelland, eds.), p. 77–94. North Atlantic Marine Mammal Commission Scientific Publications, Tromsø, Norway.

McClelland, G., J. Melendy, J. Osborne, D. Reid, and S. Douglas.
2005. Use of parasite and genetic markers in delineating populations of winter flounder from the central and south-west Scotian Shelf and north-east Gulf of Maine. J. Fish Biol. 66:1082–1100.

McClelland, G., R. K. Misra, and D. J. Martell.
2000. Spatial and temporal distributions of larval sealworm (*Pseudoterranova decipiens*, Nematoda: Anisakinae), in *Hippoglossoides platessoides* (Pleuronectidae) in eastern Canada from 1980 to 1990. ICES J. Mar. Sci. 57:69–88.

Melendy, J., G. McClelland, and T. Hurlbut.
2005. Use of parasite tags in delineating stocks of white hake (*Urophycis tenuis*) from the southern Gulf of St. Lawrence and Cape Breton Shelf. Fish. Res. 76: 392–400.

Minet, J-P.
1975. Data on the biology of American plaice from the southern bank of Newfoundland and from the Cape Breton shelf. Rev. Trav. Inst. Peches Marit. Nantes. 38: 343–434.

Neter, J., W. Wassermann, and M. H. Kutner.
1985. Applied linear statistical models: regression, analysis of variance, and experimental design, 1127 p. Richard Irwin Inc., Homewood, IL.

Olson, R. E., and I. Pratt.
1971. The life cycle and larval development of *Echinorhynchus lageniformis* Ekbaum, 1938 (Acanthocephala: Echinorhynchidae). J. Parasitol. 57:143–149.

Platt, N. E.
1975. Infestation of cod (*Gadus morhua* L.) with the larvae of codworm (*Terranova decipiens*) and herringworm, *Anisakis* sp. (Nematoda: Ascaridata) in North Atlantic and Arctic waters. J. Appl. Ecol. 12:437–450.

Power, A. M., J. A. Balbuena, and J. A. Raga.
2005. Parasite infracommunities as predictors of harvest location of bogue (*Boops boops* L.): a pilot study using statistical classifiers. Fish. Res. 72:229–239.

Powles, P.
1965. Life history and ecology of American plaice, (*Hippoglossoides platessoides* F.) in the Magdalen Shallows. J. Fish. Res. Board Can. 22:565–596.

Rohde, K.
2005. Marine Parasitology, 565 p. Commonwealth Scientific and Industrial Research Organisation Publishing, Collingwood, Victoria, Australia.

Scott, J. S.
1975. Geographic variation in incidence of trematode parasites of American plaice (*Hippoglossoides platessoides*) in the Northwest Atlantic. J. Fish. Res. Board Can. 32:547–550.

Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219:1–731.

Sokal, R. R., and F. J Rohlf.
1969. Biometry, 797 p. W.H. Freeman, San Francisco, CA.

Stott, W., M. M. Ferguson, and R. F. Tallman.
1992. Genetic population structure of American plaice (*Hippoglossoides platessoides*) from the Gulf of St. Lawrence, Canada. Can. J. Fish. Aquat. Sci. 49:2538–2545.

Swain, D. P., G. A. Chouinard, R. Morin, and K. F. Drinkwater.
1998. Seasonal variation in the habitat associations of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 55: 2548–2561.

Tallman, R. F.
1991. Causes of within season decline in the size at age of American plaice, *Hippoglossoides platessoides*. *In* The Gulf of St. Lawrence: small ocean or big Estuary? (J. C. Therriault, ed.), p. 269–275. Can. Spec. Pub. Fish. Aquat. Sci. 113.

Titus, K., J. A. Mosher, and B. K. Williams.
1984. Chance corrected classification for use in discriminant analysis: ecological applications. Am. Midl. Nat. 111:1–7.

Williams, H., and A. Jones.
1994. Parasitic worms of fish, 593 p. Taylor and Francis Ltd., London, England.

Williams, H. H., K. MacKenzie, and A. M. McCarthy.
1992. Parasites as biological indicators of the population biology, migrations, diet, and phylogenetics of fish. Rev. Biol. Fish. 2:144–176.

Wolfgang, R. W.
1955. Studies of the trematodes *Stephanostomum baccatum* (Nicoll, 1907) III. Its life cycle. Can. J. Zool. 33:113–128.

Zubchenko, A. V.
1985. Parasitic fauna of American plaice (*Hippoglossoides platessoides*) from the Northwest Atlantic. J. Northw. Atl. Fish. Sci. 6: 165–171.

Implications of substrate complexity and kelp variability for south-central Alaskan nearshore fish communities

Judy Hamilton

Kachemak Bay National Estuarine Research Reserve
95 Sterling Highway, Suite 2
Homer, Alaska 99603

Email address: judy_hamilton@fishgame.state.ak.us

Brenda Konar

School of Fisheries and Ocean Sciences
University of Alaska Fairbanks
245 O'Neill Building
Fairbanks, Alaska 99775

Abstract—Understanding the interactions between kelp beds and nearshore fish is essential because anthropogenic changes and natural variability in these beds may affect available habitat for fishes. In this study fish communities were investigated in south-central Alaska kelp beds characterized by a range of substrate complexity and varying densities of both perennial understory kelps and annual canopy kelps. Many of the observed fish species, as well as understory and canopy kelps, were positively associated with structurally complex substratum. Targeted canopy and understory kelp beds supported seasonal populations of adult and juvenile Pacific cod (*Gadus macrocephalus*), rockfishes (*Sebastes* spp.), and year-round populations of greenlings (*Hexagrammos* spp.). Monthly changes in kelp and fish communities reflected seasonal changes; the densities of some species were greatest during periods with higher temperatures. This work illustrates the importance of structurally complex kelp beds with persistent understory kelp populations as important fish habitat for several commercially and recreationally important fishes.

Manuscript submitted 10 September 2004 to the Scientific Editor.

Manuscript approved for publication 29 August 2006 by the Scientific Editor.

Fish. Bull. 105:189–196 2007).

Marine macroalgal communities in the shallow, rocky, nearshore zones are among the most productive aquatic biomes on earth and provide important habitat for invertebrates, fishes, and marine mammals (Steneck et al., 2002). Although the importance of kelp bed variability (including kelp density, distribution, and species composition) to fishes has been demonstrated in Alaskan waters (Dean et al., 2000; Hegwer, 2003; Hamilton, 2004; Calvert, 2005), the role of seasonality in these habitats is poorly understood, particularly in regions with seasonal extremes, such as the subarctic (but see Calvert, 2005). Furthermore, although the persistence and stability of kelp beds are at least partly determined by suitable space and substratum type (Dayton, 1985), the importance of overall habitat complexity (i.e., kelp cover and substrate topography) to kelp-associated fish species has not been investigated in Alaska.

Previous studies in Alaskan kelp beds have shown positive correlations between the presence of fishes and the density (or biomass) of understory algae (Dean et al., 2000; Hegwer, 2003; Hamilton, 2004). Researchers elsewhere have also agreed with these findings (Dayton, 1985) but have demonstrated relationships between fish density or biomass and the relative abundance of the canopy kelp *Macrocystis pyrifera* (Bodkin, 1986; Carr, 1994). *Macrocystis* forms dense stands that are generally stable and provide persistent habitat; beds composed of this perennial species exhibit relatively little seasonal and annual variation in structure (Dayton, 1985; Steneck et al., 2002). In contrast, northern Pacific canopy kelps are annuals (*Alaria fistulosa* and *Nereocystis luetkeana* [hereafter *Nereocystis*]) that afford much less midwater structure. As a result, vertical relief in northern Pacific kelp beds is often seasonally restricted to, and is more consistently provided by, physical structure of the seafloor and the perennial understory kelp species. The importance of physical structure (described by the measures of rugosity, substrate size, and verticality) to temperate and tropical reef fish assemblages has been documented (Aburto-Oropeza and Balart, 2001; Garcia-Charton and Perez-Ruzafa, 2001), but little is known about the importance of the physical structure of kelp and substrate to fishes in the northern Pacific rocky nearshore zones.

The objectives of this study were to assess relationships of fish to habitat structure and to seasonal variability in kelp communities. We determined the relationship of fishes to habitat structure (classified according to rugosity, size of substrate, and verticality) and kelp densities. Because north Pacific macroalgal communities vary

seasonally with the growth and senescence of annual kelps, changes in the kelp communities were correlated with associated fish abundances.

Materials and methods

Study sites

This study was conducted in Kachemak Bay, the southernmost inlet on the western shore of the Kenai Peninsula, in south-central Alaska. Ten sites were chosen based on their structural characteristics and the presence of kelp communities (Fig. 1). All sites contained understory kelp, providing varying degrees of macroalgal cover, and five sites contained the canopy-forming kelp *Nereocystis*. A distance of at least 200 m (predominantly sandy bottom) separated all sites from each other. Sites were situated at a water depth of approximately 7 m.

Study design

At each site, transects (n=3) were surveyed monthly to quantify kelp densities and fish presence between May 2002 and September 2003. A haphazard starting point was selected for each transect from which a random direction was taken. Although visibility varied among sampling periods, transects were surveyed when visibility was at least a transect width (2 m on each side) or more and therefore such visibility was not included in the analyses. Because of turbidity and poor visibility at this site, MacDonald Spit was not sampled in July and November 2002 and Anisom Point was not sampled in October 2002. Each survey had two components (a kelp and a fish survey), which were conducted concurrently by two separate divers.

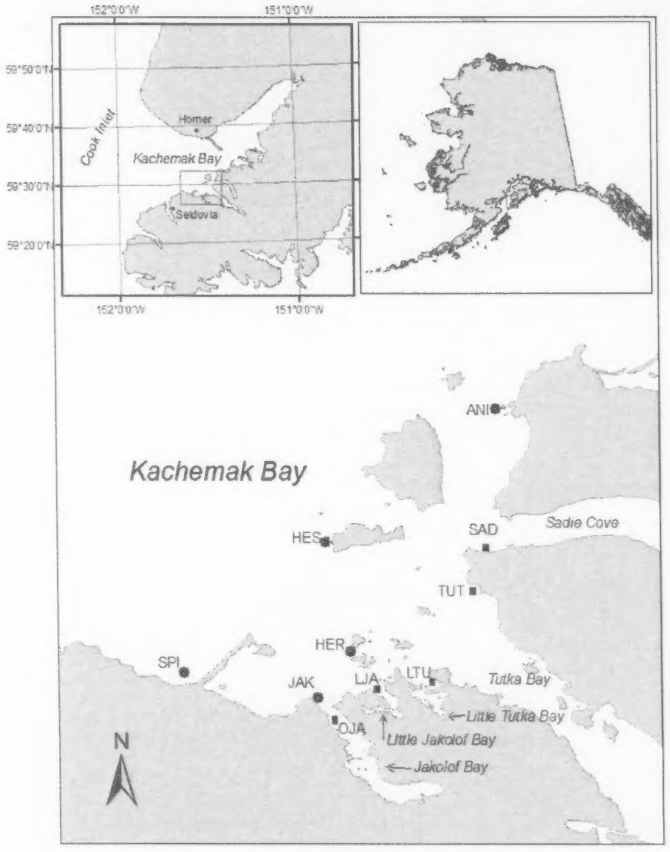


Figure 1

Location of Kachemak Bay and study sites. Sites characterized by high structural complexity of the substratum are denoted with a circle and low structural complexity sites are denoted with a square. Study sites are abbreviated as follows: ANI=Anisom Point; HER=Herring Islands; HES=Hesketh Island; JAK=Jakolof Bay; LJA=Little Jakolof Bay; LTU=Little Tutka Bay; OJA=Outside Jakolof Bay; SAD=Sadie Cove; SPI=MacDonald Spit; and TUT=Tutka Bay.

Physical habitat variables

Physical habitat variables (rugosity, substrate size, and verticality) were measured once for each site in September 2003. Rugosity and substrate size were measured for every quadrat at all sites during September 2003. Rugosity provides a measure of habitat complexity on a small spatial scale and is defined as the ratio of the true distance contour along the bottom to a one-meter horizontal distance (Leum and Choat, 1980). Rugosity was measured by using a 1-m bar with a series of 5-mm links attached at one end. The bar was held horizontally with the link end resting on the substrate. The links were then draped along the substrate beneath the bar. These links were counted and a rugosity measure was calculated for each quadrat and averaged per transect. Substrate size was determined by measuring the diameter of samples of the bottom relief (e.g., sand, cobble, bedrock) that composed greater than 50% of the quadrat (Garcia-Charton and Perez-Ruzafa, 2001). When no substrate type dominated, the percentages and sizes of each substrate type were noted. These measurements were categorized from one (sand or silt) to five (bedrock) and an average value was calculated for each site. Verticality, a subjective measure ranging from one (for low structural relief) to five (high), was assigned to each site (Bodkin, 1986). Monthly water temperature was also measured at each site.

Surveys of kelp and fish

For surveys of kelp, randomly placed 0.25-m^2 quadrats (n=10) were examined per 120-m^2 transect. All understory kelps in each quadrat were counted and identified to species. Because all understory kelp species were structurally similar (in size and overall shape), they were grouped as "annual" (*Costaria costata, Cymathere triplicata,* and *Laminaria saccharina,*) or "perennial" (*Agarum clathratum, L. bongardiana, and L. yezoensis*) understory for statistical analyses. All data collected in May 2002 were omitted from the analyses involving kelp because understory data for that month were incomplete. Analyses were conducted on the average understory kelp densities per transect to enable comparison with the relatively sparse densities of the canopy kelp and fish communities. Because *Nereocystis* was relatively rare, all individuals were counted within each 120-m^2 band transect.

For fish surveys, all fishes observed within each transect and within one meter of the bottom (30 m×4 m× 1 m=120 m^3) were enumerated and identified to species whenever possible. Because few fishes were observed, the three most abundant families (Hexagrammidae, Scorpaenidae, and Gadidae) were analyzed by family group. All other fishes were rarely observed and were grouped as "other fishes" for the analyses.

Statistical analyses

Statistical analyses were performed by using multivariate approaches and linear models with STATISTICA vers. 6 (Statsoft, Tulsa, OK). Cluster analyses were used to examine site variability in the kelp and fish communities and how this variability relates to structural complexity. Averages of all data were calculated by site across month and year for the ordination analyses. Kelp and fish densities were considered by species with the physical variables of rugosity, substrate size, and verticality. The Bray and Curtis dissimilarity coefficient (Bray and Curtis, 1957) was used and the Euclidean distance was calculated for physical variables, kelp, and fish. Water temperature did not vary among sites within months and was not used in our analysis. A one-way ANOVA was used for temporal variation of water temperature. Partial correlation analysis (with Pearson's correlation coefficient, r) was performed between kelp groups (based on average annual understory, perennial understory, and canopy kelp densities [no./120 m^2]) and physical habitat data (rugosity, substrate size, and verticality: average values per 120 m^2; water temperature: °C per month) while controlling for potentially intercorrelating variables. These results were considered significant at α<0.05. Because of the low number of fish observed, fish counts were converted to presence or absence data and logistic regression was applied. Independent variables were the four log-transformed physical variables (rugosity, substrate size, and verticality: $\log_{10}$ [average values per 120 m^2]; temperature: $\log_{10}$ [value per month],) and the three log-transformed kelp groups (annual understory kelp, perennial understory kelp, and canopy kelp: $\log_{10}$ [number of kelps per 120 m^2]). Analyses were conducted separately for each fish family that composed at least 20% of total abundance (Hexagrammidae, Scorpaenidae, and Gadidae).

Results

Physical habitat variables

Substrate in the study sites varied from complex (rocky outcrops, large boulders, and bedrock) to homogeneous (small cobble and sand). The ten sites were partitioned by clustering techniques into two general structural complexity groups based on dissimilarities among the three measured structural characteristics (rugosity, substrate size, and verticality; Fig. 2A). Water temperature varied significantly among months ($F_{12,456}$=1983.2, P<0.001). Temperature ranged from 1.8°C in winter to 11.0°C in summer and was the only physical variable that did not vary among sites. Water temperatures also differed significantly between years ($F_{1,456}$=1028.6, P<0.001), and were higher in 2003 than 2002.

Surveys of kelp and fish

A comparison of cluster dendrograms revealed patterns of spatial variation among the kelp and fish groups that mirrored the substrate trends. When all biological data (understory and canopy kelp densities and fish presence) were averaged across months and years, five sites grouped with higher counts of kelp and fish exhibited the greatest structural complexity (Fig. 2, B [kelp] and C [fish]). Similarly, three of the structurally homogenous sites were grouped consistently with lower values for both kelp and fish. Two sites (LJA and OJA) showed inconsistencies in these groupings. Little Jakolof Bay (with a lower complexity designation) was in the higher macroalgal count group but in the lower fish abundance group. Outside Jakolof Bay (with a higher complexity designation) was in the lower density groups for both kelp and fish.

Kelp communities were variable in species composition and density over space and time and understory kelp communities were considerably denser than the canopy kelp. Understory kelps were present every month and perennial kelp dominated in all months except late October 2002 (Fig. 3). The annual understory kelp *C. costata* contributed at most 2% to the annual kelp relative abundance in any month, whereas *L. saccharina* composed at least 75%. Annual understory kelps were found in greatest densities during periods with warmer water temperatures; perennial kelps, however, were not significantly correlated with temperature (Table 1). Perennial understory kelps were found on all transects; an overall equal contribution was made by *A. clathratum* and the perennial *Laminaria* species (*L. bongardiana* and *L. yezoensis*, densities lumped together). Both annual and perennial understory kelps were found in

greatest densities in sites with higher values for rugosity and verticality, although, curiously, not for substrate size (Table 1). Five sites (ANI, HER, HES, OJA, and SPI) contained *Nereocystis* in 2002, compared to two sites (HER and SPI) in 2003. Canopy kelp persisted throughout the winter at one site (HER). The greatest number of canopy kelp individuals was observed in October 2002, the lowest densities (fewer than 5 *Nereocystis*/120 m^2 transect) were observed from November through April, and no canopy kelp was observed in May 2003 (Fig. 4). Canopy kelp was more abundant during months with higher water temperatures and in sites with larger substrate and greater vertical relief, but, unlike the understory kelp, was negatively correlated with rugosity (Table 1).

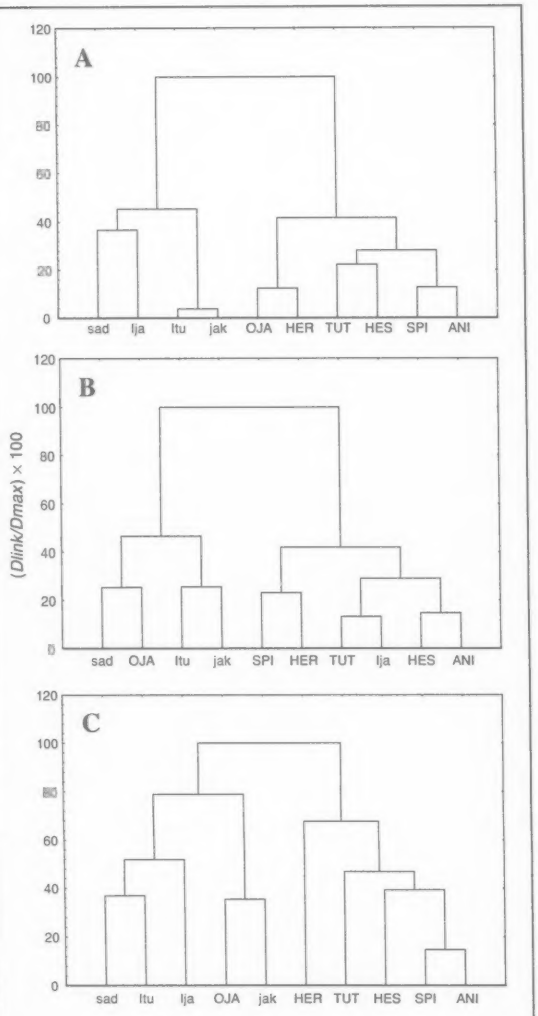


Figure 2

Cluster dendrograms based on percent dissimilarities of variables among sites. (**A**) Structural habitat descriptors (rugosity, substrate size, and verticality); (**B**) Kelp communities; and (**C**) Fish communities. Site abbreviations indicate relative structural complexity (lower case=low complexity; upper case=high complexity. Study sites are abbreviated as follows: ANI=Anisom Point; HER=Herring Islands; HES=Hesketh Island; JAK=Jakolof Bay; LJA=Little Jakolof Bay; LTU=Little Tutka Bay; OJA=Outside Jakolof Bay; SAD=Sadie Cove; SPI=MacDonald Spit; and TUT=Tutka Bay.

The presence of some fishes was associated with season, year, physical habitat characteristics, and kelp. Four hundred twenty-two fishes representing 15 species from eight families were sighted on 34% (n=171) of transects surveyed. Three families (Hexagrammidae [greenlings], Scorpaenidae [rockfishes], and Gadidae [codfishes]) each composed at least 20% of the total abundance and together accounted for more than 80% of all fishes sighted. Infrequently sighted fishes included those in the families Pholidae (gunnels, 6%), Cottidae (sculpins, 3%), Pleuronectidae (flatfishes, 2%), and others (including ronquils, searchers, and unidentified fishes, 5%). Fish presence varied over time (Table 2); more fishes were sighted in 2003 (2.59 ±6.92 fish/transect) than in 2002 (0.63 ±0.96 fish/transect). More fish (considering all fish species pooled across months, years, and sites) were seen during periods with higher temperatures and in sites characterized by larger substrate and greater densities of annual understory and canopy kelp (Table 2). Greenlings (primarily kelp greenling [*Hexagrammos decagrammus*]) accounted for the majority of sightings (35% of total abundance) and their presence did not differ among months (Table 2). Greenlings were most commonly seen in sites with low rugosity values and larger substrate (i.e., boulder to bedrock), and during periods with warmer water temperatures and higher densities of annual understory kelps.

Schooling species, such as rockfishes (primarily the black rockfish [*S. melanops*]) and adult Pacific cod (*Gadus macrocephalus*), were observed infrequently. However, these groups accounted for the greatest number of fish seen on any one transect and exhibited the greatest variability in sightings per month in the fish groups, primarily during summer 2003 (Fig. 5). There was no difference in the presence of rockfishes among months, but there were significant temporal differences for codfishes (Table 2). Considering the major families observed in this study, only the presence of rockfishes showed significant annual variability (Table 2)—more in 2003 (1.23 ±5.83 fish/transect) than in 2002 (0.08 ±0.42 fish/transect). Both rockfishes and codfishes were most commonly seen during periods with higher water temperatures (Table 2). Although these results are based only on sightings of adult fishes, large schools (thousands of individuals) of juvenile codfishes (predominately *G. macrocephalus*) were observed at all sites during August and September 2002. The juvenile codfish schools observed in summer 2003

Table 1

Partial correlation analysis (Pearson's correlation coefficient, r) between physical variables and kelp groups (n=473 transects). Values are considered significant at $P < 0.05$. Rugosity provides a small-scale measure of habitat complexity and is the ratio of the true distance contour along the bottom to a one-meter horizontal distance. Substrate size is based on the average diameter of the substrate comprising the majority of a 0.25-m^2 quadrat. Verticality was assigned to each site on the basis of overall vertical relief.

Kelp group	Temperature	Rugosity of substrate	Substrate size	Verticality of substrate
Canopy	0.18	−0.32	0.29	0.09
	P<0.001	P<0.001	P<0.001	P<0.001
Annual understory kelp	0.17	0.16	0.01	0.16
	P=0.001	P<0.001	P=0.790	P<0.001
Perennial understory kelp	0.02	0.27	−0.05	0.26
	P=0.685	P<0.001	P=0.325	P<0.001

were composed of much fewer individuals (at most, tens of individuals/school). These juvenile codfishes were not included in any analyses in our study because of difficulties in accurately quantifying them.

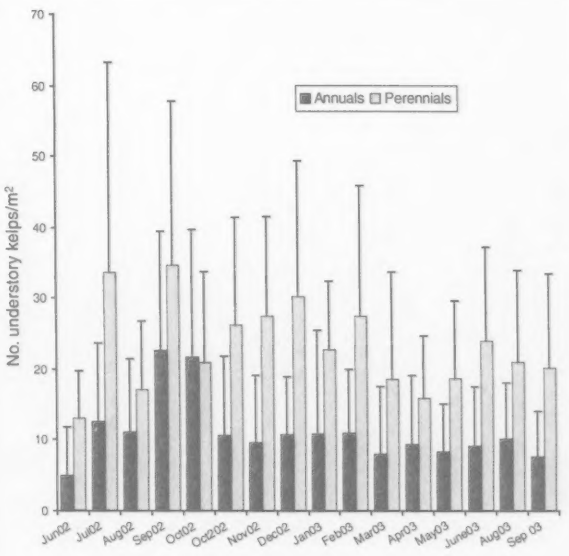


Figure 3

Monthly variation in the density (no. of plants/m^2 ±standard error) of understory kelp groups. n = 503 transects. Because surveys were conducted during alternate neap tide cycles throughout the 17 month study, two surveys occurred, at least partly, during October 2002.

Discussion

Structural habitat complexity is important to both fish and kelps in that greater physical habitat complexity is associated with greater overall densities of fish in these communities. In particular, greenlings associated most consistently with kelp beds that had a predominately rocky (i.e., large cobble/bedrock) and structurally complex bottom habitat. The association of the dominant fish species in our study with relatively larger substrate and higher rock relief may indicate that south-central Alaska kelp-bed fishes follow the same trend (of a strong association of fish with kelp and rocky substrate relief) documented elsewhere. For example, in California kelp beds, significant correlations exist between fish density and bottom relief (Ebeling et al., 1980; Bodkin, 1986). However, rockfishes in Puget Sound inhabited low-relief rocky kelp beds during summer (Matthews, 1990) and in Prince William Sound were positively associated with relief (Dean et al., 2000). Rockfishes and codfishes in the present study were never associated with any bottom structure, perhaps because of the sporadic sightings of these species. The lack of association of rockfishes and codfishes with any physical habitat variables or kelp may reflect the transient nature and seasonal association of these fishes with kelp. However, the rarity of any fishes observed higher than one meter above the substratum in the present study indicates that bottom structure may be important to the fishes observed in our study, if perhaps indirectly, by also being appropriate substratum for kelp habitat.

The variability of Alaska kelp communities and associated fish populations may be partially attributable to the extreme seasonal nature of the northern environment. Increased sightings of fish during periods characterized by warmer water indicate seasonal variability in fish communities associated with kelp communities. For example, although greenlings were observed in the shallow, rocky nearshore sites during every month in the present study, rockfishes and codfishes were rarely observed except in summer. Healthy understory kelp populations exist in this area on rocky substratum at depths of up to 16 m (first author, personal observ.) and fish populations may shift seasonally to similar

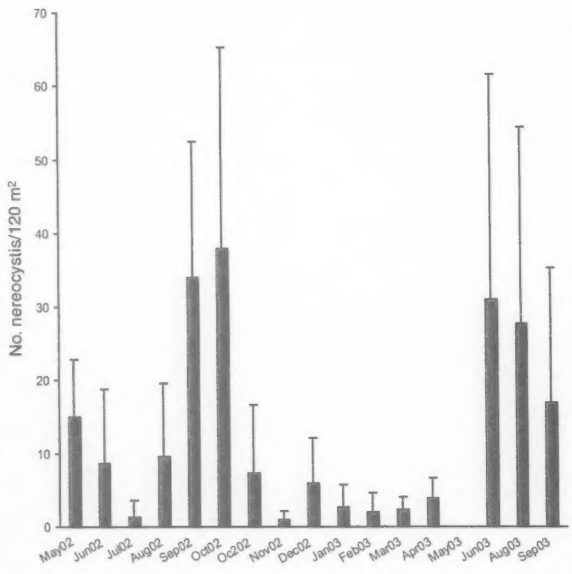


Figure 4

Monthly mean *Nereocystis luetkeana* density (no. of *Nereocystis*/120 m^2 ±standard error). The mean was averaged across the five sites initially containing canopy. n = 248 transects.

habitats in adjacent, deeper water. Puget Sound rockfishes tend to move to shallower water in summer and deeper water in winter (Moulton and Miller[1]), possibly avoiding increased storm surge during winter months. Fish communities inhabiting seasonally and annually variable kelp beds in the north Pacific must be capable of enduring a wider variety of environmental variables over the course of a season, year, or lifetime than those occupying the relatively stable, perennial canopy-dominated kelp beds of more temperate zones. The importance and magnitude of seasonal cues vary among kelp and fish species throughout their ranges and the cues include temperature, photoperiod, turbidity, increased frequency of storms and surge in winter, and prey and nutrient availability (Ebeling et al., 1980, Dayton, 1985). However, the thresholds of many environmental factors are to some extent temperature-dependent (Dayton, 1985), providing an easily quantified surrogate variable for seasonality in the present study. Kelp beds (and associated fishes) at the

[1] Miller, B. S., and L. L. Moulton. 1988. Characterization of Puget Sound fishes for the EPA Bay Program, p. 77–84. *In* Proceedings, First Annual Meeting on Puget Sound Research, vol. 1, Seattle, WA, March 18–19, 1988. Puget Sound Action Team, Office of the Governor, P.O. Box 40900, Olympia WA 98504-0900.

Table 2

Logistic regression results on the presence of fishes by families and by total abundance. Only families composing greater than 20% of the total fish abundance are included. Independent variables are time (n=503 transects for tests of "month" or n=208 transects for test of "year," the comparison of June to September of years 2002 and 2003), kelp densities (canopy kelp and annual and perennial understory kelp groups; n=473 transects), and physical habitat variables (water temperature, rugosity, substrate size, and verticality). Only significant values (P<0.05) are reported.

Analysis group	Independent variable	Parameter estimate	Standard error	Wald's χ^2	P-value
Hexagrammidae	Annual kelp understory	0.62	0.17	12.65	<0.001
	Water temperature	4.26	0.91	22.15	<0.001
	Rugosity	–2.48	1.15	4.66	0.031
	Substrate size	1.90	0.47	16.11	<0.001
Scorpaenidae	Year	0.64	0.29	4.67	0.031
	Water temperature	9.00	3.00	13.00	< 0.001
Gadidae	Month	0.27	0.08	12.19	0.001
	Water temperature	4.28	1.62	6.96	0.008
Total fish	Month	0.08	0.03	10.19	0.001
	Year	0.28	0.13	4.61	0.032
	Canopy	0.66	0.32	4.37	0.037
	Annual understory	0.21	0.10	3.99	0.046
	Water temperature	5.12	0.78	43.13	<0.001
	Substrate size	0.80	0.38	4.49	0.034

northern edge of their range are subject to wide fluctuations in all of these factors, as well as wide inter-annual variation in intensity and duration of seasonal factors. It is these extremes that make studying these habitats difficult or impossible during all but summer months and result in the paucity of consistent seasonal data in northern Pacific systems.

Aerial surveys of kelp beds in Kachemak Bay during three consecutive summers (2000–2002) showed significant differences in size, location, and presence of *Nereocystis* canopy (Schoch and Chenelot, 2004), illustrating great interannual variability that may be apparent on relatively short temporal scales. Such variability was also observed in the present study, in that three of five sites originally containing canopy kelp did not recruit *Nereocystis* juveniles the second summer. Although this canopy kelp species is considered an annual, we observed *Nereocystis* individuals reproducing into a second summer.

Our findings of relatively more fishes inhabiting *Nereocystis* beds than understory-only kelp beds indicates that areas characterized by enhanced *Nereocystis* growth may have greater fish densities. In one northern California study, densities of kelp greenling in *Nereocystis* beds were four times greater than in the present study (Bodkin, 1986). *Nereocystis* beds in California were similarly more important to rockfishes (Bodkin, 1986; Love et al., 1991) than understory kelp alone. However, the existence of high understory kelp densities in the canopy-containing sites may be of greater importance to fishes than the canopy itself. In our study sites, both the greenlings and grouped fishes were positively associated with densities of annual understory. In addition, fishes in the present study were usually observed in close association with the understory and substratum as has been typical in other south-central Alaska studies (Rosenthal[2], Dean et al., 2000). The perennial-dominated understory of south-central Alaska kelp beds may provide a degree of habitat stability for some fishes for at least part of the year.

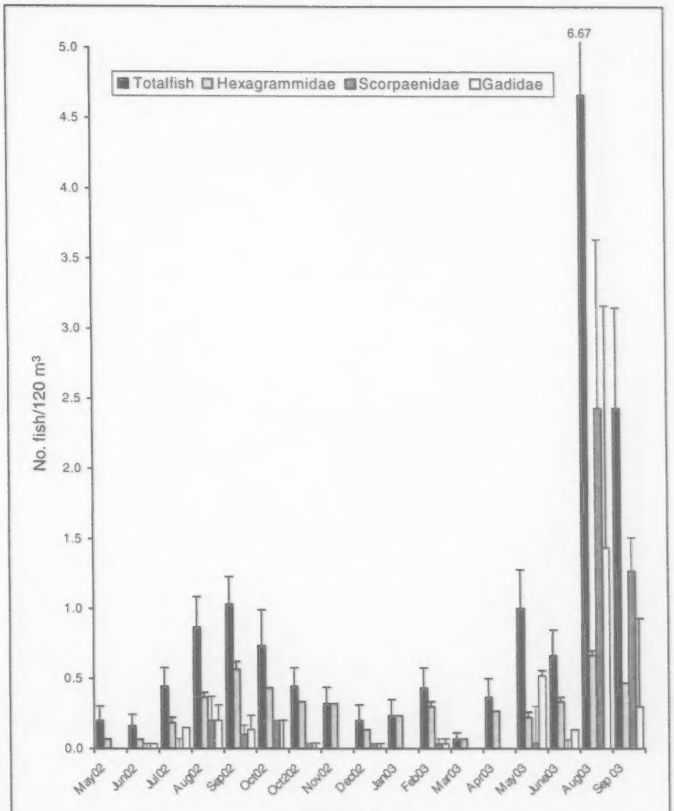


Figure 5

Monthly variation of major fish families (no. of fish/120 m³ ±standard error) averaged across sites. Only families comprising greater than 20% of total density were included. n = 503 transects.

It is difficult to account for all factors influencing a natural system, particularly without knowing the recent history of the community. Because little is known about interactions between kelp and fish communities and their natural variability in south-central Alaska, investigation of more obvious, small-scale processes over an entire year is necessary. Physical factors, such as size of the kelp beds and related edge effects of the habitat, salinity fluctuations and freshwater runoff, degree and direction of exposure to light and tidal currents, and the frequency of storm events may play a significant role in structuring these dynamic communities. In addition, biological factors that may influence algal community structure include inter- and intra-species competition and herbivory. A growing body of evidence points to the importance of temporal and spatial scales in ecological processes (i.e., Dayton and Tegner, 1984; Wiens and Addicott, 1986; Foster, 1990). The structurally complex kelp beds surveyed in the present study appear to provide critical habitat throughout the year for greenling species. However, this habitat is also seasonally important to rockfishes and codfishes (both adult and juvenile).

[2] Rosenthal, R. J. 1979. A preliminary assessment of composition and food webs for demersal fish assemblages in several shallow subtidal habitats in lower Cook Inlet, Alaska, 58 p. *In* Final report by Dames and Moore, Inc., 800 Cordova Street, Suite 101, Anchorage, AK 99501, for Alaska Department of Fish and Game. Commercial Fisheries Division, 211 Mission Rd., Kodiak, Alaska 99615.

This work provides a description and baseline information on the structural characteristics of south-central Alaska's nearshore kelp beds and associated fish communities, and provides insight on the importance of seasonality. These findings may enable managers to identify potentially important nearshore fish habitat from relatively easily quantified structural habitat variables. The identification of critical habitat areas for juvenile and adult fishes is essential for sustainable management, and the importance of habitat structure in and influence of seasonality on these habitats has been further illuminated by this work.

Acknowledgments

This publication is the result of research sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA 16RG2321 (project number R/31-09) and from the University of Alaska with funds appropriated by the state. We wish to thank S. Hills, G. Haas, and A. Blanchard, as well as numerous reviewers, divers, and logistical supporters for their priceless assistance.

Literature cited

Aburto-Oropeza, O., and E. F. Balart.
2001. Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. Mar. Ecol. 22:283–305.

Bodkin, J. L.
1986. Fish assemblages in *Macrocystis* and *Nereocystis* kelp forests off central California. Fish. Bull. 84:799–807.

Bray, J. R., and J. T. Curtis.
1957. An ordination of the upland forest communities of southern Wisconsin. Ecol. Mono. 27:325–329.

Calvert, E. L.
2005. Kelp beds as fish and invertebrate habitat in southeastern Alaska. M.S. thesis, 113 p. Univ. Alaska Fairbanks, Juneau, AK.

Carr, M. H.
1994. Effects of macroalgal dynamics on recruitment of a temperate reef fish. Ecology 75:1320–1333.

Dayton, P. K., and M. J. Tegner.
1984. Catastrophic storms, El Nino, and patch stability in a southern California kelp community. Science 224:283–285.

Dayton, P. K.
1985. Ecology of kelp communities. Annu. Rev. Ecol. Sys. 16:215–245.

Dean, T. A., L. Haldorson, D. R. Laur, S. C. Jewett, and A. Blanchard.
2000. The distribution of nearshore fishes in kelp and eelgrass communities in Prince William Sound, Alaska: associations with vegetation and physical habitat characteristics. Environ. Biol. Fishes 57:271–287.

Ebeling, A. W., R. J. Larson, W. S. Alevizon, and R. N. Bray.
1980. Annual variability of reef fish assemblages in kelp forests off Santa Barbara, California. Fish. Bull. 78:361–367.

Foster, M. S.
1990. Organization of macroalgal assemblages in the northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia 192:21–33.

Garcia-Charton, J. A., and A. Perez-Ruzafa.
2001. Spatial pattern and the habitat structure of a Mediterranean rocky reef fish local assemblage. Mar. Biol. 138:917–934.

Hamilton, J. A.
2004. Kelp bed variability and fish population dynamics in Kachemak Bay, Alaska. M.S. thesis, 57 p. Univ. Alaska Fairbanks, Fairbanks, AK.

Hegwer, C. L.
2003. Seasonal abundance and diversity of nearshore fishes around Steller sea lion haulouts of Kodiak Island. M.S. thesis, 76 p. Univ. Alaska Fairbanks, Fairbanks, AK.

Leum, L. L., and J. H. Choat.
1980. Density and distribution patterns of the temperate marine fish *Cheliodactylus spectabilis* in a reef environment. Mar. Biol. 57:327–337.

Love, M. S., M. H. Carr, and L. J. Haldorson.
1991. The ecology of substrate-associated juveniles of the genus *Sebastes*. Environ. Biol. Fishes 30:225–243.

Matthews, K. R.
1990. A comparative study of habitat use by young-of-the-year, subadult, and adult rockfishes on four habitat types in central Puget Sound. Fish. Bull. 88:223–239.

Schoch, G. C., and H. Chenelot.
2004. The role of estuarine hydrodynamics in the distribution of kelp forests in Kachemak Bay, Alaska. J. Coast. Res. 45:179–194.

Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, and M. J. Tegner.
2002. Kelp forest ecosystems: biodiversity, stability, resilience, and future. Environ. Cons. 29:436–459.

Wiens, J. A., and J. F. Addicott.
1986. Overview of the importance of spatial and temporal scale in ecological investigations. *In* Community ecology (J. Diamond, and T. J. Case, eds.), p. 145–153. Harper and Row, New York, NY.

Genetic variability in spotted seatrout (*Cynoscion nebulosus*), determined with microsatellite DNA markers

Rocky Ward (contact author)
Kevin Bowers
Rebecca Hensley
Brandon Mobley
Ed Belouski

Email address for R. Ward: rward@usgs.gov

Texas Parks and Wildlife Department
Coastal Fisheries Division
4200 Smith School Road
Austin, Texas 78744

Present address for R. Ward: Northern Appalachian Research Laboratory
USGS/Leetown Science Center
176 Straight Run Rd.
Wellsboro, Pennsylvania 16901

Abstract—Variation in the allele frequencies of five microsatellite loci was surveyed in 1256 individual spotted seatrout (*Cynoscion nebulosus*) obtained from 12 bays and estuaries from Laguna Madre, Texas, to Charlotte Harbor, Florida, to St. John's River on the Florida Atlantic Coast. Texas and Louisiana collection sites were resampled each year for two to four years (1998–2001). Genetic differentiation was observed. Spotted seatrout from Florida waters were strongly differentiated from spotted seatrout collected in Louisiana and Texas. The greatest genetic discontinuity was observed between Tampa Bay and Charlotte Harbor, and Charlotte Harbor seatrout were most similar to Atlantic Coast spotted seatrout. Texas and Louisiana samples were not strongly structured within the northwestern Gulf of Mexico and there was little evidence of temporal differentiation within bays. These findings are contrary to those of earlier analyses with allozymes and mitochondrial DNA (mtDNA) where evidence of spatial differentiation was found for spotted seatrout resident on the Texas coast. The differences in genetic structure observed among these markers may reflect differences in response to selective pressure, or may be due to differences in underlying genetic processes.

Manuscript submitted 23 February 2006 to the Scientific Editor's Office.

Manuscript approved for publication 11 September 2006 by the Scientific Editor.

Fish. Bull. 105:197–206 (2007).

Spotted seatrout (*Cynoscion nebulosus*) support an important recreational fishery in the northern Gulf of Mexico and along the U.S. Atlantic Coast. Management of this fishery is multijurisdictional, employing a variety of strategies including reduction or elimination of commercial exploitation, adjustments of recreational fish-size limits and bag limits, closed seasons, and artificial spawning and stocking of fish (Vanderkooy and Muller, 2003). Effective management requires an understanding of the ecology, life history, and genetic structuring of a species. Understanding genetic population structure is important to every aspect of fishery management but is especially critical when stocking fish is the chosen management strategy. Stocking without regard for existing genetic variability within and among populations places the genetic integrity of the targeted species at risk (Allendorf et al., 1986). Genetic population structuring may be evidence of adaptation to past environmental differences, whereas genetic variability may enable a population to meet future environmental challenges.

Evidence of population structuring in spotted seatrout has been gained through morphological, physiological, and genetic examinations. Regional differences have been found in otolith and scale structure, growth rate (Iverson and Tabb, 1962; however, see Murphy and Taylor, 1994 for a different interpretation), and in reproductive physiology (Brown-Peterson et al., 2002). Each of these studies found evidence of biologically significant regional differentiation—a finding consistent with observations of limited movement within and between bays (Music, 1981; Overstreet, 1983; Baker and Matlock, 1993) and between bays and adjacent nearshore waters (Baker et al., 1986).

Studies of genetic markers generally support the existence of population structuring among spotted seatrout in the northern Gulf of Mexico. Studies examining protein variation found evidence of weak (Ramsey and Wakeman, 1987; King and Pate, 1992) to strong (Weinstein and Yerger, 1976) population subdivision. The King and Pate (1992) study found indications of clinal variation in mean heterozygosity and in alleles of the aspartate aminotransferase-2 locus, indicating possible adaptation to environmental gradients on the Texas coast (King and Zimmerman, 1993). In each of the allozyme studies indications of isolation by distance were found, as was found in a survey in which mitochondrial DNA was used (mtDNA; Gold et al., 1999). In the

mtDNA study, significant heterogeneity was found in haplotype frequencies among collection sites, indicating that spotted seatrout were spatially differentiated. In contrast, Gold et al. (2003) found no significant differences in microsatellite DNA allele frequency among spotted seatrout inhabiting Texas bays. A similar study of microsatellite variation among spotted seatrout of the U.S. Atlantic and Florida Gulf coasts (employing different loci from those of Gold et al., 2003) found extensive spatial differences that coincided with known zoogeographic barriers (Wiley and Chapman, 2003). Surprisingly, the Indian River spotted seatrout sample on Florida's Atlantic coast was genetically more similar to the Choctawhatchee sample from the Florida Panhandle than to more northerly Atlantic Coast samples. The overall pattern that emerges from applications of molecular markers to the examination of spatial genetic variability in spotted seatrout is mixed. Most studies have found limited gene flow between adjacent bays and moderate population subdivision, and patterns of differentiation that may be described as "isolation by distance." The failure of the Gold et al. (2003) to find statistically significant genetic subdivision is surprising, given that studies employing allozymes and mtDNA have been successful in discerning genetic structuring and given that microsatellites are considered to be among the most capable genetic markers at resolving population level differentiation (Wright and Bentzen, 1994). Gold et al. (2003) focused on the northwestern Gulf of Mexico, and their geographically limited examination may have restricted the ability of the marker to discern patterns in the spatial variability of spotted seatrout. It is also possible that underlying genetic properties of the markers accounted for the differences in observed variation, or that some markers (i.e., allozymes) were able to detect genetic adaptation to environmental gradients which microsatellites, assumed to be selectively neutral, were not.

The present study is an attempt to re-examine genetic variability in spotted seatrout in the northern Gulf of Mexico. As did Gold et al. (2003) (who also examined a portion of the present data), we used microsatellite markers. Samples from Louisiana and the Gulf and Atlantic coasts of Florida were added in an attempt to give a greater spatial perspective that may be useful in evaluating the observed genetic variability among populations. In addition, samples from multiple years were included for Texas and Louisiana bays, allowing for evaluation of the stability and robustness of detected genetic structure.

Materials and methods

A total of 1256 individuals were examined. Sample collection sites are shown in Figure 1. All Texas sites were sampled in three consecutive years, 1998–2000, except Corpus Christi Bay which was sampled across four years, 1998–2001. The Louisiana site was sampled in 1999 and in 2000, and the Florida sites were sampled only in 2000. Texas and Florida samples were obtained through routine resource sampling efforts of Texas Parks and Wildlife Department and Florida Department of Natural Resources personnel, respectively, and Louisiana samples were donated by licensed recreational anglers. Soft dorsal-fin tissue was removed from the fish, placed in 95% ethanol, and stored at room temperature until processed. Genomic DNA was extracted by using the PureGene DNA isolation kit and protocols (Gentra Systems, Inc., Minneapolis, MN).

Primers designed to amplify three microsatellites (*Soc*12, *Soc*50, and *Soc*243) originally developed for red drum (*Sciaenops ocellatus*) by Turner et al. (1998) were employed. Two additional primer pairs (*Cne*133 and *Cne*133′) were designed by sequencing products of the *Soc*133 (Turner et al., 1998) forward and reverse primers and then identifying internal primer sequences that amplified separate repeat regions within the original *Soc*133 amplicon. Primer sequences for *Cne*133 and *Cne*133′ and protocols for amplification and interpretation are discussed in Gold et al. (2003).

Summary statistics were generated by using the Microsoft Excel add-on Microsatellite Toolkit (Park, 2001) and ARLEQUIN, version 2.001 (Schneider et al., 2000), which was also employed to test frequencies for deviations from Hardy-Weinberg equilibrium by using exact tests performed with Markov-chain randomization (Guo and Thompson, 1992). Permutations with 1000 resamplings (Manly, 1991) were used to generate probability values (P) for each test of Hardy-Weinberg equilibrium for each microsatellite locus in each sample. ARLEQUIN was also used to test for linkage between microsatellite loci, and significance of P-values was estimated by 1000 resamplings. Critical values for interpreting significance levels for simultaneous inferential comparisons were adjusted by using the sequential Bonferroni approach (Rice, 1989).

Allelic distribution homogeneity of each microsatellite was assessed with exact tests implemented with the statistical package GENEPOP, version 3.4 (Raymond and Rousset, 1995), and significance was estimated by permutation with 1000 resamplings for each comparison. Population subdivision was estimated with Weir and Cockerham's (1984) theta (θ) as generated in FSTAT, version 2.9.3 (Goudet, 1995), and a bootstrap procedure in FSTAT was employed to calculate a 95% confidence interval (CI). Although the use of theta is contigent on the assumption of an infinite-alleles mutation model (Kimura and Crow, 1964), it has been shown to compare favorably with other measures of genetic subdivision when employed with microsatellite data (Ruzzante, 1998). The significance of population differentiation across all loci was estimated as the combined probability of P-values for Fisher's exact tests for individual loci. Separate analyses were made for data sets that comprised 13 samples defined by site and collection date and 13 samples defined by site alone, with date combined across all year classes.

A hierarchical analysis of gene diversity was performed by using the analysis of molecular variance

model (AMOVA; Michalakis and Excoffier, 1996) in ARLEQUIN (Excoffier et al., 1992). The components of genetic diversity attributable to variance between regions (Atlantic versus Gulf of Mexico), variance among sampling sites within regions, temporal variance among years within sampling sites, and variance among individuals within samples were estimated. The significance of each variance component was tested with nonparametric permutation procedures (~1000 permutations; Excoffier et al., 1992). In addition, genetic differentiation among all collection sites for each sampling year and between pairs of populations within sampling years was estimated by using the theta statistic of Weir and Cockerham (1984) accessed on FSTAT (Goudet, 1995).

Cavalli-Sforza and Edwards' chord distance (D_C; Cavalli-Sforza and Edwards, 1967) was used to reconstruct phylogenetic relationships among collection sites. Estimations of D_C were obtained with the statistical package NJBPOP (Cornuet et al., 1999). Takezaki and Nei (1996) found D_C to be a better estimate of genetic divergence with microsatellite DNA data than with measures based on the step-wise mutation model. This estimate is not based on the assumption of a constant population size or a constant mutation rate among loci (Takezaki and Nei, 1996) and appears to accurately resolve closely related populations (Paetkau et al., 1997; Angers and Bernatchez, 1998). A phenogram was generated from the chord-distance matrix with the neighbor-joining (N-J) algorhithm. Robustness of each node was evaluated by bootstrapping over loci for 2000 replications (Hedges, 1992) with the SEQBOOT program on PHYLIP, version 3.5c (Felsenstein, 1995). The PHYLIP program CONSENSE then was used to generate a consensus tree which was drawn with the program TREEVIEW (Page, 1996).

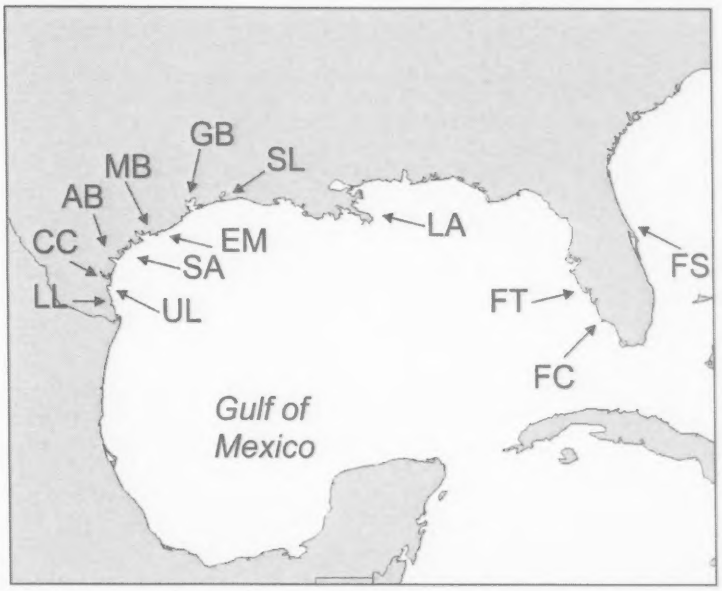


Figure 1

Sampling localities for spotted seatrout (*Cynoscion nebulosus*) examined from the northern Gulf of Mexico and the Atlantic Coast of Florida. LL = lower Laguna Madre; UL = upper Laguna Madre; CC = Corpus Christi Bay; AB = Aransas Bay; SA = San Antonio Bay; MB = Matagorda Bay; EM = east Matagorda Bay; GB = Galveston Bay; SL = Sabine Lake; LA = Grand Isle, Louisiana; FT = Tampa Bay, Florida; FC = Charlotte Harbor, Florida; FS = St. John's River, Florida.

Results

The number of alleles per sample (Table 1) exceeded those reported for the same loci in red drum (*Sciaenops ocellatus*), the species of origin for the markers (Turner et al., 1998). Mean observed heterozygosity (H_O) ranged from 0.21 to 0.39, and there were no statistically significant deviations from Hardy-Weinberg expectations at any locus and sample combination after Bonferroni adjustment. Without the Bonferroni correction, allele frequencies at 16 of 165 comparisons would have failed to meet expectations. This included all loci except *Soc*243, which was observed to be in Hardy-Weinberg equilibrium in all samples. *Soc*012 most often failed to meet Hardy-Weinberg expectations; six of 33 samples were out of equilibrium before Bonferroni adjustment. Observed heterozygosity was lower than expected in 14 of the 16 locus-and-sample combinations that failed to meet Hardy-Weinberg expectation before adjustment. Statistically significant linkage disequilibrium was noted for one pair of loci in one sample (*Cne*133′ with *Soc*12 in sample GB99) after Bonferroni adjustments. If the unadjusted critical value (α=0.05) was applied, 15 of 330 comparisons were statistically significant. Interestingly, the associated loci *Cne*133 and *Cne*133′ did not exhibit linkage disequilibrium for any sample.

After Bonferroni adjustment, exact tests for allele distribution homogeneity across all 33 samples demonstrated statistically significant differentiation for all microsatellite loci except *Soc*50, which approached statistical significance (P=0.05). All theta estimates were significantly greater than zero after Bonferroni adjustments, as was the overall theta of 0.116 (95% CI, 0.007–0.073; P<0.001), indicating significant genetic differentiation across both the spatial and temporal dimensions sampled in this study. When spatial samples were collapsed to form 13 spatial samples, all loci except *Soc*50 exhibited statistically significant deviations from

Table 1

Summary statistics for spotted seatrout (*Cynoscion nebulosus*) samples included in a survey of microsatellite variation. n = number of individuals in sample; n_a = number of alleles; P_{HW} = probability of meeting Hardy-Weinberg expectations (with Bonferri-corrected critical value of $\alpha = 0.0003$.

Sample location	Sample acronym	n		*Soc* 12	*Soc* 50	*Soc* 243	*Cne* 133	*Cne* 133′
St. Johns River, Florida 2000	FS00	26	n_a	3	2	3	3	3
			P_{HW}	0.32	0.19	0.13	1.00	0.11
Charlotte Harbor, Florida 2000	FC00	22	n_a	3	2	2	3	2
			P_{HW}	0.18	1.00	1.00	1.00	1.00
Tampa Bay, Florida 2000	FT00	40	n_a	3	2	2	4	2
			P_{HW}	0.18	1.00	1.00	0.23	0.25
Grand Isle, Louisiana 1999	LA99	60	n_a	3	2	3	4	3
			P_{HW}	0.46	1.00	0.86	1.00	0.05
Grand Isle, Louisiana 2000	LA00	39	n_a	3	3	2	3	2
			P_{HW}	0.69	0.21	0.51	1.00	1.00
Sabine Lake, Texas 1998	SL98	23	n_a	3	2	2	3	2
			P_{HW}	0.157	1.00	1.00	0.04	1.00
Sabine Lake, Texas 1999	SL99	36	n_a	3	3	3	3	2
			P_{HW}	0.61	0.07	1.00	0.30	1.00
Sabine Lake, Texas 2000	SL00	30	n_a	3	3	3	3	2
			P_{HW}	1.00	0.22	0.34	1.00	1.00
Galveston Bay, Texas 1998	GB98	28	n_a	4	2	2	3	2
			P_{HW}	0.03	1.00	1.00	1.00	1.00
Galveston Bay, Texas 1999	GB99	37	n_a	3	3	3	3	2
			P_{HW}	0.61	0.07	1.00	0.30	1.00
Galveston Bay, Texas 2000	GB00	40	n_a	3	5	3	3	3
			P_{HW}	0.03	0.32	0.39	0.80	1.00
E. Matagorda Bay, Texas 1998	EM98	33	n_a	4	2	2	3	2
			P_{HW}	0.91	0.29	0.72	0.27	1.00
E. Matagorda Bay, Texas 1999	EM99	40	n_a	4	2	2	3	2
			P_{HW}	0.47	0.02	0.15	0.01	1.00
E. Matagorda Bay, Texas 2000	EM00	40	n_a	3	2	2	3	2
			P_{HW}	0.33	1.00	0.72	0.21	0.25
Matagorda Bay, Texas 1998	MB98	40	40	3	3	3	3	2
			P_{HW}	0.22	0.01	0.67	1.00	1.00
Matagorda Bay, Texas 1999	MB99	40	40	3	2	2	3	2
			P_{HW}	0.36	0.25	0.51	1.00	1.00
Matagorda Bay, Texas 2000	MB00	40	40	3	2	3	4	2
			P_{HW}	0.36	1.00	0.56	1.00	1.00
San Antonio Bay, Texas 1998	SA98	40	n_a	3	3	3	3	2
			P_{HW}	0.03	0.12	0.37	1.00	1.00
San Antonio Bay, Texas 1999	SA99	40	n_a	3	3	3	3	3
			P_{HW}	0.84	0.02	0.39	0.68	1.00
San Antonio Bay, Texas 2000	SA00	40	n_a	4	4	2	3	2
			P_{HW}	0.01	0.39	1.00	1.00	1.00
Aransas Bay, Texas 1998	AB98	40	n_a	3	2	3	3	3
			P_{HW}	1.00	0.18	0.67	0.16	1.00
Aransas Bay, Texas 1999	AB99	39	n_a	4	3	3	4	2
			P_{HW}	0.43	1.00	0.67	0.57	1.00
Aransas Bay, Texas 2000	AB00	40	n_a	3	2	3	4	2
			P_{HW}	0.04	0.06	0.39	0.19	1.00
Corpus Christi Bay, Texas 1998	CC98	40	n_a	3	2	3	3	2
			P_{HW}	0.61	1.00	0.57	1.00	1.00
Corpus Christi Bay, Texas 1999	CC99	50	n_a	3	4	3	3	2
			P_{HW}	0.04	<0.01	0.81	0.17	1.00

continued

Table 1 (continued)

Sample location	Sample acronym	n		*Soc* 12	*Soc* 50	*Soc* 243	*Cne* 133	*Cne* 133′
Corpus Christi Bay, Texas 2000	CC00	40	n_a	3	2	4	3	3
			P_{HW}	0.10	0.33	0.25	1.00	0.19
Corpus Christi Bay, Texas 2001	CC01	35	n_a	3	4	4	4	3
			P_{HW}	0.59	0.02	0.71	0.74	1.00
Upper Laguna Madre, Texas 1998	UL98	40	n_a	3	2	3	3	2
			P_{HW}	0.05	1.00	0.33	1.00	1.00
Upper Laguna Madre, Texas 1999	UL99	40	n_a	3	3	4	3	3
			P_{HW}	0.07	0.05	0.16	0.04	1.00
Upper Laguna Madre, Texas 2000	UL00	40	n_a	3	4	4	4	2
			P_{HW}	0.31	1.00	0.36	1.00	1.00
Lower Laguna Madre, Texas 1998	LL98	38	n_a	4	3	2	3	2
			P_{HW}	0.06	0.13	1.00	0.79	0.01
Lower Laguna Madre, Texas 1999	LL99	40	n_a	3	3	5	4	2
			P_{HW}	0.55	1.00	1.00	0.04	1.00
Lower Laguna Madre, Texas 2000	LL00	40	n_a	3	2	3	3	2
			P_{HW}	0.84	1.00	0.31	1.00	0.39

homogeneous allele distributions and the overall test was significant (P_{exact}<0.001). Estimated theta values were statistically significant after Bonferroni adjustment, except *Cne*133′. The overall estimate of theta (θ=0.057, 95% CI, 0.005–0.062) was lower than the estimate including both spatial and temporal dimensions (θ=0.116), indicating that temporal differences likely contributed to overall population differentiation in spotted seatrout.

Analysis of molecular variance indicated a statistically significant 4.11% of the among-sample genetic variance was attributable to differences between Gulf and Atlantic samples (P=0.04). Statistically significant variance was also detected among sampling sites within the Gulf of Mexico (0.49% of the total variance, P<0.001). No significant genetic variance attributable to temporal differences was found within bays (P=0.42). An overall F_{ST} of 0.046 was estimated, which was statistically significant (P<0.001).

We found no significant differences among Texas bays in the 1998 collections (Table 2). In 1999, spotted seatrout from Texas and Louisiana were not differentiated except for the Galveston Bay samples that differed significantly from all other samples. Analyses of year 2000 collections, which included samples from Texas, Louisiana, and Florida, revealed differences between Florida samples and all samples from Louisiana and Texas. The Louisiana sample differed from most Texas samples, and within Texas most samples were genetically undifferentiated, except for samples Galveston Bay which were significantly different from those of all bays, except Sabine Lake and Corpus Christi. Finally, the upper and lower Laguna Madre samples were statistically different from each other. Temporally, the only statistically significant differences among years were seen among Louisiana and Galveston Bay samples. The overall theta within sampling years ranged from less than 0.006 in 1998 to 0.080 in 2000, perhaps reflecting the increased genetic variability introduced by the Florida samples in the 2000 data set. The statistically insignificant differentiation among sampling years within bays, with the exception of the Louisiana and Galveston Bay, supports the notion that temporal differentiation, at least on the limited scale reported in our study, may be ignored and temporal samples can be collapsed within bays. The genetic structure of spotted seatrout in Galveston Bay is highly differentiated, both temporally and spatially, showing significant differences in 1999 and 2000 with almost all other bays.

The topology of the neighbor-joining tree based on D_C for 34 site and year groups (Fig. 2) was poorly supported by bootstrap replications and demonstrated little correspondence to geographic and temporal patterns. An exception was the separation of samples FC00 and FS00 (Charlotte Bay and St. John's River, FL, respectively; acronyms are defined in Table 1) from samples collected in the northern and western Gulf. When groupings were collapsed across years (Fig. 3), the distinctiveness of the Florida samples from the southern Gulf Coast and the Atlantic Coast continued to be supported. Spotted seatrout from Florida's Tampa Bay (FT00) were found to be more closely related to spotted seatrout from Louisiana and Texas than to spotted seatrout in the other Florida samples. Texas and Louisiana samples formed a well-differentiated grouping; however, within that grouping, there was little correspondence between genetic differentiation and geographic location. One exception was the south coast of Texas (Corpus Christi Bay and the upper and

lower Laguna Madre), which formed a weakly supported clade.

A statistically significant ($P<0.001$) correlation between D_C and geographic distance was observed ($r=0.90$) and thus supported the isolation-by-distance hypothesis. The greatest geographic distance between adjacent collection sites was observed between Charlotte Harbor and St. John's River; however, when the St. John's River sample was excluded from the analysis, a significant positive relationship was still evident ($r=0.80$, $P<0.001$). The correlation between D_C and geographic distance within the western Gulf of Mexico (Texas and Louisiana) remained positive ($r=0.42$) and statistically significant ($P=0.05$).

Discussion

Spotted seatrout inhabiting a series of sites from the lower Laguna Madre of Texas to St. John's River on the Atlantic Coast of Florida were genetically differentiated by analyses of allele frequencies of five microsatellite markers. Samples from Florida waters were strongly differentiated from spotted seatrout from Louisiana and Texas, and the statistically significant correlation between geographic distance and genetic distance was due primarily to these differences. Within Florida, the Charlotte Harbor spotted seatrout is genetically more similar to the Atlantic Coast spotted seatrout from St. John's River than to the neighboring Tampa Bay spotted seatrout, which is genetically more similar to Texas and Louisiana than to other Florida fish of the same species. Differences in allele frequency between Charlotte Harbor and Tampa Bay samples represented the greatest discontinuity observed in this study. This putative population structure is congruent with Wiley and Chapman's (2003) findings of distinct population subdivision among Atlantic Coast spotted seatrout, although details of that structure may be difficult to reconcile. Wiley and Chapman (2003) found spotted

Table 2

Results of tests for homogeneity in allele distributions among samples of spotted seatrout (*Cynoscion nebulosus*). Pairwise-θ estimates for 1998 samples (above diagonal), 1999 samples (below diagonal), and 2000 samples (lower matrix). θ^T is θ calculated across all sampling periods within a bay. * indicates statistical significance ($\alpha=0.05$) after adjustment for multiple comparisons (Rice, 1989). Acronyms for within-bay samples collapsed across years are the two letters (e.g., LA99+LA00=LA). Definitions for abbreviations for sample locations (LA, SL, etc.) are given in Table 1.

Sample location	LA	SL	GB	EM	MB	SA	AB	CC	UL	LL
SL	−0.007	0.000	0.026	−0.011	−0.010	−0.003	0.011	0.015	0.012	0.002
GB	0.092*	0.070*	0.000	0.019	0.010	0.009	0.006	0.009	0.004	0.029
EM	0.009	0.002	0.053*	0.000	−0.007	0.006	−0.003	0.019	0.018	0.020
MB	0.007	0.007	0.083*	0.000	0.000	−0.008	−0.001	0.002	−0.001	0.005
SA	−0.004	−0.006	0.078*	−0.001	−0.006	0.000	0.008	−0.002	−0.005	0.000
AB	0.008	0.001	0.089*	−0.004	−0.000	−0.001	0.000	0.009	0.008	0.024
CC	−0.006	−0.008	0.079*	0.001	−0.004	−0.011	−0.001	0.000	0.000	0.010
UL	0.003	−0.002	0.081*	−0.001	0.011	−0.002	0.000	0.001	0.000	0.003
LL	0.005	0.002	0.072*	−0.009	−0.006	−0.003	−0.006	−0.003	0.000	0.000

	FC	FT	LA	SL	GB	EM	MB	SA	AB	CC	UL	LL
FS	0.007	0.326*	0.108*	0.061*	0.110*	0.039*	0.077*	0.053*	0.053*	0.0532*	0.031*	0.081*
FC		0.341*	0.136*	0.077*	0.145*	0.031*	0.085*	0.054*	0.059*	0.068*	0.043*	0.081*
FT			0.245*	0.185*	0.257*	0.263*	0.195*	0.229*	0.219*	0.236*	0.288*	0.136*
LA				0.057	0.011	0.084*	0.067*	0.058*	0.039	0.029	0.093*	0.063*
SL					0.065	0.006	0.012	−0.006	0.003	−0.001	0.016	0.003
GB						0.105*	0.104*	0.083*	0.072*	0.050	0.115*	0.083*
EM							0.011	−0.003	0.004	0.004	−0.007	0.019
MB								0.009	−0.004	0.013	0.016	0.001
SA									−0.006	−0.005	0.004	0.013
AB										−0.004	0.008	0.008
CC											0.013	0.016
UL												0.034*
θ^T			0.065*	0.004	0.049*	<0.001	−0.004	−0.002	<0.001	0.013	0.001	0.013

seatrout from Indian River, Florida (which is near St. John's River), to be genetically more similar to spotted seatrout from Choctawhatchee Bay in the Florida Panhandle than to other Atlantic Coast fish of the same species. The analyses of the two studies, taken together, indicate at least two distribution breaks in the eastern Gulf and the Atlantic, the first between Georgia and the upper Atlantic Coast of Florida and a second between Charlotte Harbor and Tampa Bay. The clustering of populations observed by Wiley and Chapman (2003) between Indian River and Choctawhatchee Bay may, in light of our finding of a genetic discontinuity between the intervening Charlotte Harbor and Tampa Bay, reflect relative differences in genetic affinity discerned by the two data sets. Resolution of this possible incongruence will require examination of numerous sampling sites collected from both the Atlantic and Gulf coasts of Florida.

Spotted seatrout inhabiting the northwestern Gulf of Mexico from the Laguna Madre to Grand Isle, Louisiana, were not found to be subdivided into discernible stocks or populations and there was little indication of temporal differentiation within bays. Exceptions to this lack of temporal differentiation were seen in Galveston Bay and in Louisiana. Temporal differences in these two sites may be due to sampling error (although the *n* for each year's sample in the two sites appear to be adequate), or these two large regions may harbor populations that are temporally or spatially genetically structured. Some indications of geographically coherent spatial patterns were observed among spotted seatrout in the northwestern Gulf of Mexico. For example, there was an indication that this species on the lower coast is genetically differentiated, albeit weakly, from conspecifics inhabiting bays on the middle and upper Texas coast. This finding is similar to that found in allozyme (King and Pate, 1992) and mtDNA data (Gold et al., 1999) where differences between Laguna Madre samples and more northerly bays were observed. Galveston Bay spotted seatrout were also found to be genetically divergent, being genetically distinct from spotted seatrout in all other bays in 1999 and most bays in 2000. Galveston Bay was, in addition, one of two sites where the genetic structure of spotted seatrout was found to be temporally heterogeneous. Gold et al. (2003) found the upper Texas Coast to be a region of genetic transition; a notable shift in allele frequencies of the *Soc*201 locus was evident between Matagorda Bay and Sabine Pass—a span that includes Galveston Bay.

The lack of genetic population subdivision in the northwestern Gulf is consistent with the observed decrease in heterozygosity in relation to Hardy-Weinberg expectations. Similar heterozygote deficiencies in white seabream (*Diplodus sargus*) (Lenfant and Planes, 2002) were hypothesized to represent mixing of genetically disparate individuals during some stage of recruitment (the Wahlund effect). This phenomenon may be characteristic of many marine fishes, especially those with local populations recruited from a larval stage with highly dispersive capabilities. Spotted seatrout, due to its unique life history characteristics, is not an obvious example of a marine species expected to exhibit high gene flow. Spotted seatrout are confined to nearshore waters, spend most of their life within an estuarine habitat, and spawn and select their nursery area within the estuary (McMichael and Peters, 1989). Results of tagging studies support the hypothesis of a natal bay affinity based on spotted seatrout life history (e.g., Baker and Matlock, 1993). Stock structure among spotted seatrout was detected by the studies of morphology, physiology, (Iverson and Tabb, 1962), and genetics (Gold et al., 1999, and references therein). This population structure was not detected in the Gold et al. (2003) or the present analyses of variation in microsatellite DNA loci—markers expected to yield a high-resolution analysis of population-level genetic variability. The differences observed between microsatellite variability and that seen in allozymes (Weinstein and Yerger, 1976; Ramsey and Wakeman, 1987; King and Pate, 1992) and mtDNA (Gold et al., 1999) may reflect different evolutionary processes (Gold et al., 2003).

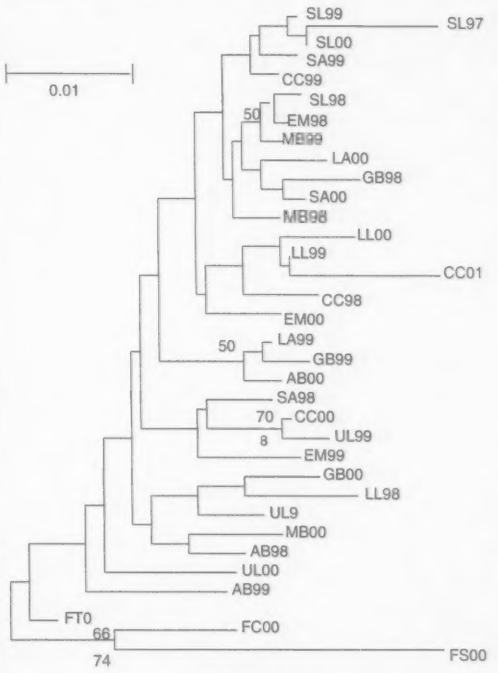


Figure 2

Cavalli-Sforza and Edwards (1967) chord distance neighbor-joining phenogram calculated for 33 spatial and temporal samples of spotted seatrout (*Cynoscion nebulosus*). Values along branches indicate bootstrap values as percentages of replicates, based on locus (above line) or individual (below line). Letter codes are defined in Table 1.

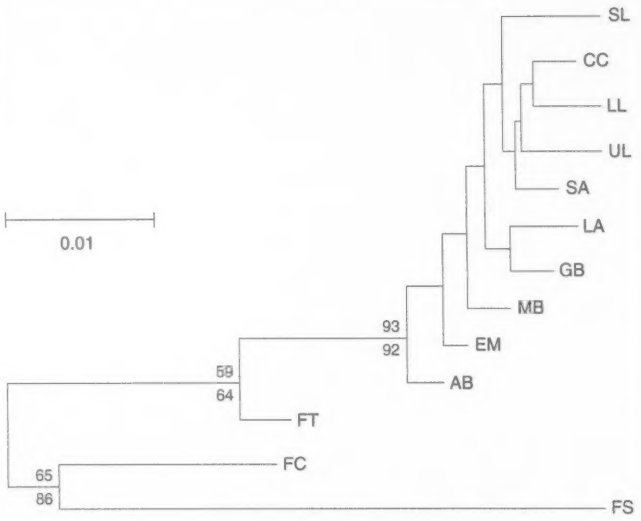


Figure 3

Cavalli-Sforza and Edwards (1967) chord distance neighbor-joining phenogram calculated for 13 spatial samples of spotted seatrout (*Cynoscion nebulosus*). Values along branches indicate bootstrap values as percentages of replicates, based on locus (above line) or individual (below line). Letter codes are defined in Table 1.

Microsatellites are assumed to be selectively neutral, whereas the allozyme and mtDNA markers used in earlier studies are potentially subject to selection and thus may present different patterns for the same region (Hellberg et al., 2002). King and Zimmerman (1993) suggested the cline in *AAT*-2 observed by King and Pate (1992) may reflect adaptation to temperature or salinity gradients along the Texas Coast. Microsatellite markers would not, in the absence of linkage to loci affected by selection, be subject to such processes. It is also possible, as Gold et al. (2003) suggested, that the earlier allozyme and mtDNA studies provided evidence, not of genetic differentiation of populations inhabiting neighboring bays, but rather of a general confirmation of the isolation-by-distance model, where greatest genetic differences are found between the most peripheral sampling sites.

Currently, about 5 million fingerling spotted seatrout are stocked per year into Texas bays and estuaries. Neither Florida nor the other states of the eastern Gulf of Mexico have implemented large-scale spotted seatrout stocking programs; however such efforts are being considered. The genetic population structure observed in studies of allozymes (Weinstein and Yerger, 1976; Ramsey and Wakeman, 1987; King and Pate, 1992) and mtDNA (Gold et al., 1999) argue for a cautious policy concerning the stocking of spotted seatrout. Gold et al. (2003) suggested the gene flow observed in microsatellite markers argued against the current Texas policy of stocking only into the bay from which broodfish were procured. Allowing stocking into both the bay of broodfish origin and into adjacent bays would meet this suggestion of simulated gene flow and still protect the putative population subdivision detected by the earlier studies. Should stocking programs in Florida or elsewhere in the northeastern Gulf be implemented, it is critical, considering the level of population subdivision observed in the present study and that of Wiley and Chapman (2003), that fine-scale genetic surveys in the eastern Gulf be accomplished. It is also obvious that inter-regional transfers of spotted seatrout should be strictly avoided.

Acknowledgments

This research was partially funded by the Federal Aid to Sportfish Restoration Program, project F-36-R. Samples were provided by staff of the Coastal Fisheries Division of Texas Parks and Wildlife Department, the Florida Fish and Wildlife Conservation Commission, and A. Landry and W. Dailey of Texas A&M University, Galveston. I. Blandon, W. Karel, and J. Burr provided laboratory assistance. A debt of gratitude is owed L. McEachron and R. Colura of Texas Parks and Wildlife Department, who supported and guided this work.

Literature cited

Allendorf, F., N. Ryman, and F. Utter.
1986. Genetics and fishery management: past, present, and future. *In* Population genetics and fishery management (N. Ryman, and F. Utter, eds.), p 1–19. Washington Sea Grant Program, Seattle, WA.

Angers, B., and L. Bernatchez.
1998. Combined use of SMM and non-SMM methods to infer fine structure and evolutionary history of closely related brook charr (*Salvelinus fontinalis*, Salmonidae) populations from microsatellites. Mol. Biol. Evol. 15:143–159.

Baker, W. B., Jr., and G. C. Matlock.
1993. Movement of spotted seatrout in Trinity Bay, Texas. Northeast Gulf Sci. 13:29–34.

Baker, W. B., Jr., G. C. Matlock, L. W. McEachron, A. W. Green, and H. E. Hegen.
1986. Movement, growth, and survival of spotted seatrout tagged in Bastrop Bayou, Texas. Contr. Mar. Sci. 29:91–101.

Brown-Peterson, N. J., M. S. Peterson, D. L. Nieland, M. D. Murphy, R. G. Taylor, and J. R. Warren.
2002. Reproductive biology of female spotted seatrout, *Cynoscion nebulosus*, in the Gulf of Mexico: differences among estuaries? Environ. Biol. Fishes 63:405–415.

Cavalli-Sforza, L. L., and A. W. F. Edwards.
1967. Phylogenetic analysis models and estimation procedures. Am. J. Human Gen. 19:233–257.

Cornuet, J.-M., S. Piry, G. Luikart, and M. Solignac.
1999. New methods employing multilocus genotypes to select or exclude populations as origins of individuals. Genetics 153:1989–2000.

Excoffier, L., P. E. Smouse, and J. M. Quattro.
1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. Genetics 131:479–491.

Felsenstein, J.
1995. PHYLIP (Phylogeny Inference Package), version 3.57c. Univ. Washington, Seattle, WA.

Gold, J. R., L. R. Richardson, and C. Furman.
1999. Mitochondrial DNA diversity and population structure of spotted seatrout (*Cynoscion nebulosus*) in coastal waters of the southeastern United States. Gulf Mex. Sci. 1999:40–50.

Gold, J. R., L. B. Stewart, and R. Ward.
2003. Population structure of spotted seatrout (*Cynoscion nebulosus*) along the Texas Gulf Coast, as revealed by genetic analysis. *In* Biology of the spotted seatrout (S. A. Bartone, ed.), p. 17–29. CRC Press, Boca Raton, FL.

Goudet, J.
1995. F-STAT (version 1.2): A computer program to calculate F-statistics. J. Hered. 86:485–486.

Guo, S., and E. Thompson.
1992. Performing the exact test of Hardy-Weinberg proportion from multiple alleles. Biometrics 48:361–372.

Hedges, S. B.
1992. The number of replications needed for the accurate estimation of the bootstrap *P* value in phylogenetic studies. Mol. Biol. Evol. 9:366–369.

Hellberg, M. E., R. S. Burton, J. E. Neigel, and S. R. Palumbi.
2002. Genetic assessment of connectivity among marine populations. Bull. Mar. Sci. 70:273–290.

Iverson, E. S. and D. C. Tabb.
1962. Subpopulations based on growth and tagging studies of spotted seatrout, *Cynoscion nebulosus*, in Florida. Copeia 1962:544–548.

Kimura, M., and J. F. Crow.
1964. The number of alleles that can be maintained in a finite population. Genetics 49:725–738.

King, T. L., and H. O. Pate.
1992. Population structure of spotted seatrout inhabiting the Texas Gulf Coast: an allozymic perspective. Trans. Am. Fish. Soc. 121:746–756.

King, T. L., and E. G. Zimmerman.
1993. Clinal variation at aspartate aminotransferase-2 in spotted seatrout, *Cynoscion nebulosus* (Cuvier), inhabiting the northwestern Gulf of Mexico. Animal Gen. 24:59–61.

Lenfant, P., and S. Planes.
2002. Temporal genetic changes between cohorts in a natural population of a marine fish, *Diplodus sargus*. Biol. J. Linn. Soc. 76:9–20.

Manly, B. J. F.
1991. Randomization and Monte Carlo methods in biology, 281 p. Chapman and Hall, New York, NY.

McMichael, R. H., Jr., and K. M. Peters.
1989. Early life history of spotted seatrout, *Cynoscion nebulosus* (Pisces: Sciaenidae), in Tampa Bay, Florida. Estuaries 12:98–110.

Michalakis, Y., and L. Excoffier.
1996. A generic estimation of population subdivision using distances between alleles with special reference to microsatellite loci. Genetics 142:1061–1064.

Murphy, M. D., and R. G. Taylor.
1994. Age, growth, and mortality of spotted seatrout in Florida waters. Trans. Am. Fish. Soc. 123:482–497.

Music, J. L., Jr.
1981. Seasonal movement and migration of spotted seatrout (*Cynoscion nebulosus*). Estuaries 4:280.

Overstreet, R. M.
1983. Aspects of the biology of the spotted seatrout, *Cynoscion nebulosus*, in Mississippi. Gulf Res. Rep. (suppl. 1):1–43.

Paetkau, D., L. P. Waits, P. L. Clarkson, L. Craighead, and C. Strobeck.
1997. An empirical evaluation of genetic distance statistics using microsatellite data from bear (Ursidae) populations. Genetics 147:1943–1957.

Page, R. D. M.
1996. TREEVIEW: an application to display phylogenetic trees on personal computers. Comp. Appl. Biosci. 12:357–358.

Park, S. D. E.,
2001. Trypanotolerance in west African cattle and the population genetic effects of selection. Ph.D. diss., 241 p. Univ. Dublin, Dublin, Republic of Ireland.

Ramsey, P. R., and J. M. Wakeman.
1987. Population structure of *Sciaenops ocellatus* and *Cynoscion nebulosus* (Pisces: Sciaenidae): biochemical variation, genetic subdivision and dispersal. Copeia 1987:682–695.

Raymond, M., and F. Rousset.
1995. GENEPOP (vers. 1.2): population genetics software for exact tests and ecumenicism. J. Genet. 86:248–249.

Rice, W. R.
1989. Analyzing tables of statistical tests. Evolution 43:223–225.

Ruzzante, D. E.
1998. A comparison of several measures of genetic distance and population structure with microsatellite data: bias and sampling variance. Can. J. Fish. Aquat. Sci. 55:1–14.
Schneider, S., D. Roessli, and L. Excoffier.
2000. ARLEQUIN, vers. 2.000: a software for population genetics data analysis. Genetics and Biometrics Laboratory, Department of Anthropology and Ecology, Univ. Geneva, CP 511 1211 Geneva 24, Switzerland.
Takezaki, N., and M. Nei.
1996. Genetic distances and reconstruction of phylogenetic trees from microsatellite DNA. Genetics 144:389–399.
Turner, T. F., L. R. Richardson, and J. R. Gold.
1998. Polymorphic microsatellite DNA markers in red drum (*Sciaenops ocellatus*). Mol. Ecol. 7:1771–1773.
Vanderkooy, S. J., and R. G. Muller.
2003. Management of spotted seatrout and fishery participants in the U.S. *In* Biology of the spotted seatrout (S. A. Bartone, ed.), p. 227–245. CRC Press, Boca Raton, FL.
Weinstein, M. P., and R. W. Yerger.
1976. Electrophoretic investigation of subpopulations of the spotted seatrout, *Cynoscion nebulosus* (Cuvier), in the Gulf of Mexico and Atlantic Coast of Florida. Comp. Biochem. Physiol. 54B:97–102.
Weir, B. S., and C. C. Cockerham.
1984. Estimating *F*-statistics for the analysis of population structure. Evolution 38:1358–1370.
Wiley, B. A., and R. W. Chapman.
2003. Population structure of spotted seatrout, *Cynoscion nebulosus*, along the Atlantic Coast of the U.S. *In* Biology of the spotted seatrout (S. A. Bartone, ed.), p. 31–40. CRC Press, Boca Raton, FL.
Wright, J. M., and P. Bentzen.
1994. Microsatellites: genetic markers for the future. Rev. Fish Biol. Fish. 4:384–388.

Review of the crevalle jacks, *Caranx hippos* complex (Teleostei: Carangidae), with a description of a new species from West Africa

William F. Smith-Vaniz (contact author)[1]

Kent E. Carpenter[2]

Email address for W. F. Smith-Vaniz: bill_smith-vaniz@usgs.gov

[1] U.S. Geological Survey
7920 NW 71st Street
Gainesville, Florida 32653
Present address: Division of Ichthyology
Florida Museum of Natural History
Dickinson Hall, Museum Road
University of Florida
Gainesville, Florida 32611-7800

[2] Department of Biological Sciences
Old Dominion University
Norfolk, Virginia 23529

Abstract—The *Caranx hippos* species complex comprises three extant species: crevalle jack (*Caranx hippos*) (Linnaeus, 1766) from both the western and eastern Atlantic oceans; Pacific crevalle jack (*Caranx caninus*) Günther, 1868 from the eastern Pacific Ocean; and longfin crevalle jack (*Caranx fischeri*) new species, from the eastern Atlantic, including the Mediterranean Sea and Ascension Island. Adults of all three species are superficially similar with a black blotch on the lower half of the pectoral fin, a black spot on the upper margin of opercle, one or two pairs of enlarged symphyseal canines on the lower jaw, and a similar pattern of breast squamation. Each species has a different pattern of hyperostotic bone development and anal-fin color. The two sympatric eastern Atlantic species also differ from each other in number of dorsal- and anal-fin rays, and in large adults of *C. fischeri* the lobes of these fins are longer and the body is deeper. *Caranx hippos* from opposite sides of the Atlantic are virtually indistinguishable externally but differ consistently in the expression of hyperostosis of the first dorsal-fin pterygiophore. The fossil species *Caranx carangopsis* Steindachner 1859 appears to have been based on composite material of *Trachurus* sp. and a fourth species of the *Caranx hippos* complex. Patterns of hyperostotic bone development are compared in the nine (of 15 total) species of *Caranx sensu stricto* that exhibit hyperostosis.

Manuscript submitted 26 June 2006 to the Scientific Editor's Office.

Manuscript approved for publication 2 October 2006 by the Scientific Editor.

Fish. Bull. 105:207–233 (2007).

Species of the *Caranx hippos* complex or crevalle jacks (Fig. 1) are fished commercially or recreationally in coastal waters throughout their range. Recognized as "superb light tackle species" by the International Game Fish Association (IGFA, 2006), they are important apex predators in inshore tropical waters—all species attaining maximum sizes approaching or exceeding 22.7 kg (50 lb). They are also commonly exhibited in public aquaria and books on marine fishes usually include accounts of them for the areas where these species are found. Despite this importance, there has been considerable confusion regarding the taxonomy and geographic distributions of these species. Gill and Kemp (2002) discussed the potentially serious implications for fishery and conservation managers of an inadequate taxonomic understanding of putatively widespread shore-fish species. Blaber (2002) noted that one of the major obstacles to ecological research in developing countries is the difficulty associated with correct identification of tropical marine and estuarine fishes, which is exacerbated by an overall decline in funding throughout the world for taxonomic research.

In a general review of the phenomenon of hyperostosis in fishes, including those of the allopatrically distributed and externally nearly identical species *Caranx hippos* (Linnaeus) (Atlantic Ocean) and *C. caninus* Günther (eastern Pacific Ocean), Smith-Vaniz et al. (1995) determined that patterns of hyperostotic bone development were often species-specific. These findings stimulated us to re-evaluate the taxonomic status of specimens from the eastern Atlantic identified as *Caranx hippos*, which we herein recognize as actually representing two species. The primary objectives of this research were to describe a new species of West African *Caranx* that has been routinely misidentified as *C. hippos*, to provide diagnoses and comparisons for all members of the *Caranx hippos* complex, and to determine their geographic distributions.

This study has been hampered by the scarcity of preserved adults of *Caranx hippos* from the eastern Atlantic. This scarcity is not surprising because natural history museums and institutional fish collections do not exist in any coastal West African country, and preservation and shipment of large fish specimens from the region

are logistically difficult. Color photographs of *Caranx hippos* provided by the International Game Fish Association and numerous colleagues indicate that adults of this species are relatively common locally, especially during October to February. We urge fishery biologists and others who have the opportunity to obtain adults of fishes that mature at relatively large sizes to help ensure that at least a few such specimens are available in major research collections.

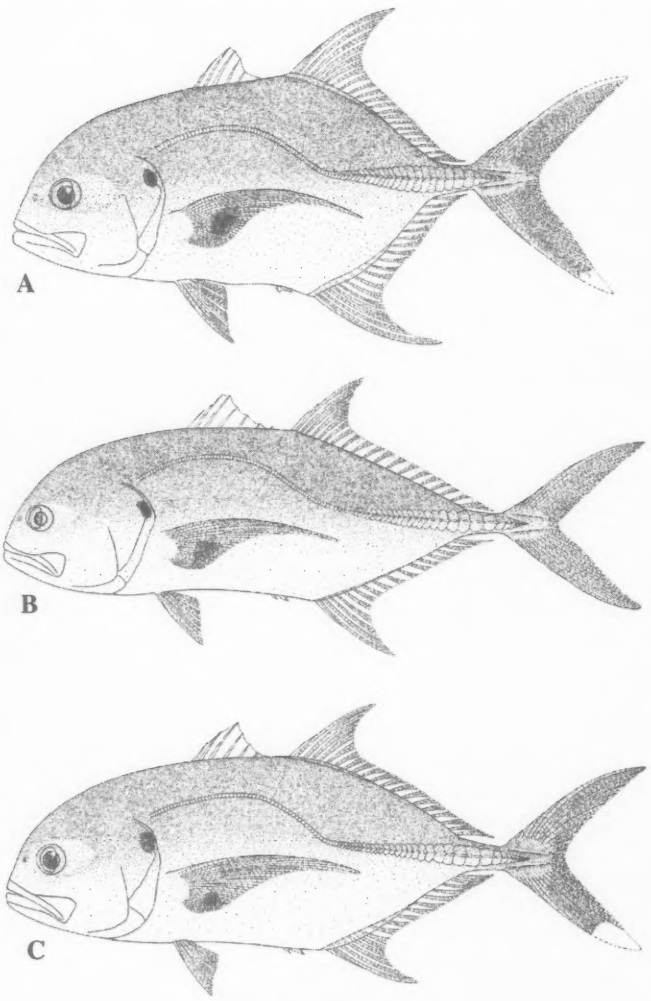


Figure 1

The *Caranx hippos* species complex: (**A**) longfin crevalle jack (*C. fischeri*), 358 mm FL, BMNH 1927.12.7.49, Ascension Island; (**B**) crevalle jack (*C. hippos*), 390 mm FL, USNM 33247, Florida, Dixie Co., Swannee River; (**C**) Pacific crevalle jack (*C. caninus*), 359 mm FL, USNM 127918, Peru, Lobos de Tierra Island. Illustrations by Tracy D. Pedersen.

Taxonomic history

The genus *Caranx* was established by Lacépède (1801, p. 57) and the type-species *Caranx carangua* Lacépède was apparently first designated by Desmarest (1856, p. 242) as *Caranx carougus* [*sic*] Bloch, which is a junior synonym of *Scomber hippos* Linnaeus. Two other generic or subgeneric names have been applied to these species (*Tricropterus* Rafinesque, 1810 and *Carangus* Girard, 1858), but both are junior synonyms of *Caranx* because the type species of these nominal taxa is also *Scomber carangus* Bloch.

Caranx hippos was first described (Linnaeus, 1766) from Carolina as *Scomber hippos*. The putative holotype, a right halfskin (Wheeler, 1985), was included in one of the last shipments of dried fish specimens sent to Linnaeus by the colonial physician Alexander Garden (Sanders, 1997). Synonyms of *Caranx hippos* (see species account) are either unnecessary replacement names or Linnaeus's original description was not considered. Nichols (1920), because his superficial description of his new Brazilian subspecies, *Caranx hippos tropicus*, was based on too few specimens, failed to appreciate the range of variation in the species, and other workers have correctly disregarded this trinominal. In his description of the eastern Pacific *Caranx caninus*, Günther (1867, 1868) did not compare this species with any other species. Jordan and Gilbert (1883), Jordan (1895), and Gilbert and Starks (1904) all concluded that this nominal species was indistinguishable from the western Atlantic *C. hippos*. In their major work on the fishes of Panama, Meek and Hildebrand (1925) also did not recognize *C. caninus* as a valid species, stating "a careful comparison of our large series from the two coasts discloses no differences of importance." Hildebrand (1946) continued to recognize fish from both oceans as conspecific. Berry (1974) stated that eastern Pacific and western Atlantic specimens of *Caranx hippos* are essentially identical. Eschmeyer and Herald (1983) stated that *C. caninus* might not be a valid species. Eschmeyer (1998)

and Castro-Aguirre et al. (1999) both treated it as a synonym of C. *hippos*; however, the former subsequently recognized *C. caninus* as a valid species (Eschmeyer[1]).

Most recent authors have recognized a single eastern Atlantic member of this species group, which has been uncritically referred to as *Caranx hippos* (Fowler, 1936; Bini, 1968; Hureau and Tortonese, 1973; Bauchot and Pras, 1980; Smith-Vaniz and Berry, 1981; Smith-Vaniz, 1986; Smith-Vaniz et al., 1990; Bauchot, 1992). In the few cases where two species were recognized (Cadenat, 1960; Blache et al., 1970; Okera, 1978), the scientific names used for both species were misapplied. The name *C. carangus* Valenciennes [*sic*] (the account given in Cuvier and Valenciennes, 1833 is not an original description) was used for the true *C. hippos* and the superficially similar new species (*C. fischeri*) was routinely misidentified as *C. hippos*.

Materials and methods

Abbreviations used for institutional depositories and cooperative organizations are as follows: American Museum of Natural History, New York (AMNH); Academy of Natural Sciences of Philadelphia (ANSP); The Natural History Museum, London (BMNH); California Academy of Natural Sciences, San Francisco (CAS, CAS-SU); Food and Agricultural Organization of the United Nations, Rome (FAO); International Game Fish Association, Dania Beach, Florida (IGFA); Institut Royal des Sciences Naturales de Belgique, Brussels (IRSNB); Musee Royal des de l'Afrique Centrale, Tervuren (MRAC); Museum National d'Histoire Naturelle, Paris (MNHN); Naturhistorisches Museum, Wien (Vienna), Austria (NMW); South African Institute of Aquatic Biodiversity (formerly J. L. B. Smith Institute of Ichthyology), Grahamstown (SAIAB); Scripps Institution of Oceanography, La Jolla (SIO); Florida Museum of Natural History, Gainesville (UF); National Museum of Natural History, Washington, D. C. (USNM); Universitat Hamburg (ISH, ZMH); Zoological Museum, University of Copenhagen (ZMUC).

Parenthetical expressions in material examined include number of specimens, if more than one, followed by the size range in millimeters fork length (FL); cleared and stained specimens are indicated as "C&S." Localities are abbreviated and listed only by major geographic areas for *Caranx caninus* and western Atlantic *C. hippos*. Except for those given in the scatter plots, measurements are of limited value in distinguishing members of the *hippos* complex (and then only for specimens >200 mm FL). Total lengths (TL) are given when that was the only length measurement reported in cited references. All measurements are in mm unless specified as cm. Measurements expressed in percent fork length or head length, are given only in the description of the new species *Caranx fischeri*. Fork length is measured from the front of the upper lip to the tip of shortest median caudal-fin ray. Body depths are measured from the anterior base of the spinous dorsal fin (D1O) to the origin of the pelvic fin (P2O) and from the anterior base of the spine at the origin of the dorsal-fin lobe (D2O) to the anterior base of the anal-fin spine at the origin of the anal-fin lobe (A2O). Lengths of the dorsal- (D2) and anal-fin (A2) bases are straight-line measurements from either the D2O or A2O to the posterior base of the terminal fin ray of the respective fin. Head length is measured from the front of the upper lip to the posterior end of the opercular flap. Snout length is measured from the anterior end of the upper lip to the anterior edge of the eye. Eye diameter is the greatest bony diameter. Upper jaw length is taken from the anterior end of the upper lip to the posterior end of the maxilla. The curved part of the lateral line is measured as a chord (straight-line distance) of the arch extending from the upper edge of the opercle to its junction with the straight part; the straight part of the lateral line is measured from its junction with the curved part to its termination on the caudal-fin base (end of last scute). Scutes are defined as scales that have a raised horizontal ridge or a small to moderate projecting spine on the posterior margin ending in a point not exceeding a 120° angle; for detailed description and illustrations of scute formation and development in *Caranx crysos* (Mitchill) see Berry (1960). All scutes were counted, including those extending onto the caudal-fin base. Pectoral-fin ray counts do not include the dorsal-most spine-like element. Gill raker counts are from the first gill arch (usually on the right side), and the raker at the angle is included in the lower-limb count; rudimentary gill rakers, with the diameter of their bases greater than their height, are defined as tubercles or short rakers. The anterior dorsal-fin pterygiophore formula indicates the interdigitation pattern of supraneurals and pterygiophores within interneural spaces; neural spines are indicated by slashes, supraneural (predorsal) bones by an "S," pterygiophores by "2" (pterygiophores with two supernumerary rays and a serially associated ray) or "1" (no supernumerary ray and one serially associated ray).

Results

Taxonomy and distributions

Some recent authors (Amezcua-Linares, 1996; Randall, 1996; McBride and McKown, 2000) still follow Briggs (1960) in erroneously reporting a worldwide distribution in tropical and subtropical latitudes for *Caranx hippos*, although Nichols (1920) had correctly concluded that records of the species from the Indian and western Pacific oceans were based on misidentifications. Other authors (Talwar and Kacker, 1984; Krishnan and Mishra, 1994; Mishra et al., 1999; Khan, 2003;

[1] Eschmeyer, W. N. Catalog of fishes, on-line edition. Website: http://www.calacademy.org/research/ichthyology/catalog/ (accessed June 2006).

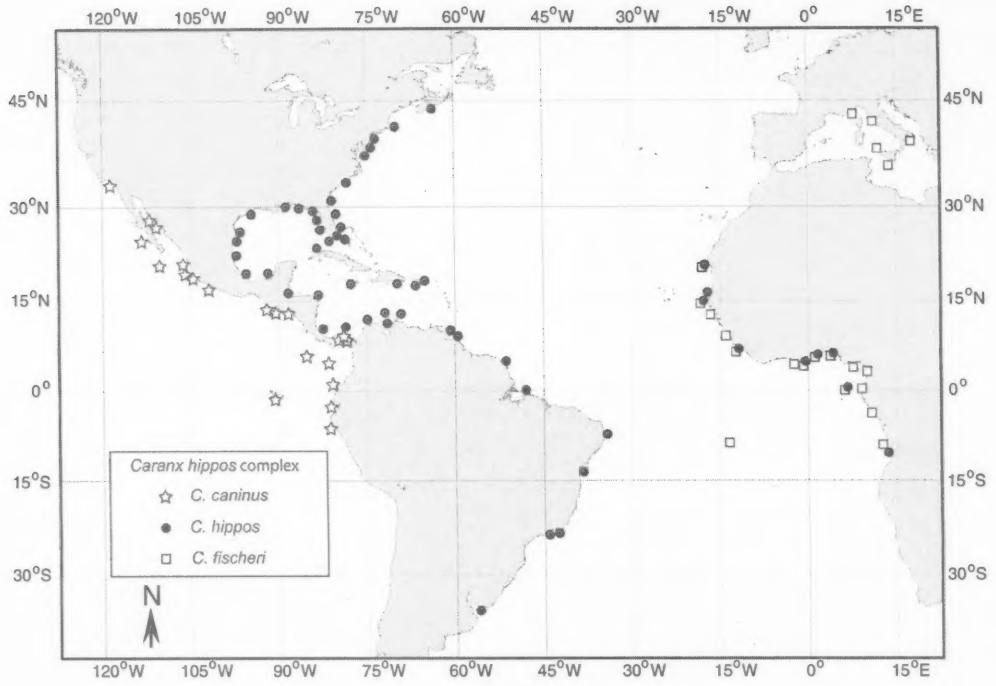


Figure 2

Distribution of members of the crevalle jack (*Caranx hippos*) complex: (Mediterranean locality records for longfin crevalle jack (*C. fischeri*) are based solely on literature reports; discussion of geographic distribution appears in individual species accounts).

Mishra and Krishnan, 2003) reported *C. hippos* as *C. carangus* (Bloch) from the Indian Ocean based on misidentifications of *Caranx heberi* (Bennett). What was once considered to be a single widespread species is herein recognized as consisting of three species (Fig. 2). For almost a century, most ichthyologists and fishery biologists who have worked on West African crevalle jacks have failed to distinguish the new species *Caranx fischeri* described herein from *C. hippos*, although both species are commonly taken together.

Adults of *Caranx hippos* from opposite sides of the Atlantic Ocean are indistinguishable externally but exhibit consistent differences in the degree of development of the hyperostosis in the first dorsal-fin pterygiophore and neural spines of some of the anterior vertebrae (see "Geographic variation" in *C. hippos* species account). Although we consider these predictable ontogenetic and consistent site-specific patterns obvious evidence of genetic divergence associated with bone metabolism, an important consideration is the unknown functional significance of hyperostosis. In light of this, we believe it would be premature to recognize the eastern Atlantic population of *C. hippos* as taxonomically distinct. No formal change in classification should be made in the absence of collaborative molecular data.

The *Caranx hippos* complex

The *C. hippos* species complex can be diagnosed by the following combination of characters: a pair of strong symphyseal dentary canines (Fig. 3); breast naked ventrally except for a small oblong patch of prepelvic scales (Fig. 4) which forms at about 30 mm FL; rounded black blotch on the lower rays of the pectoral fin in adults; large black opercular spot; and vertebrae 10 precaudal + 14 caudal. Only the black blotch on the pectoral fin is unique to these species. Adults of the horse-eye jack, *Caranx latus* Agassiz, occasionally have a somewhat similarly placed dusky blotch on the pectoral fin (although the dark area is different in character and never as well defined as in *C. hippos*), and this similarity in appearance has occasionally resulted in field misidentifications, especially by scuba divers unfamiliar with both species. The typical breast squamation pattern of the *C. hippos* species complex is not duplicated in any other Atlantic or eastern Pacific species of *Caranx*, although it occurs in three Indo-west Pacific species: commonly in *C. ignobilis* (Forsskål) and *C. papuensis* Alleyne and Macleay, and less frequently in *C. heberi*. Dentition has been used as an important diagnostic character of carangid genera, but comparison of the dentition of a large number of

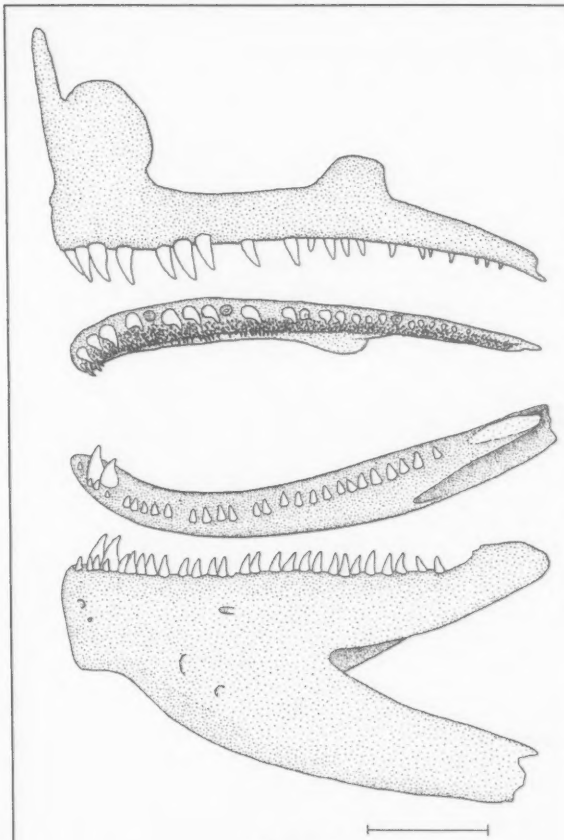


Figure 3

Dentition of crevalle jack (*Caranx hippos*), UF 69645, 180 mm FL, Florida, Gulf of Mexico: premaxilla (above), dentary (below); scale bar = 5 mm.

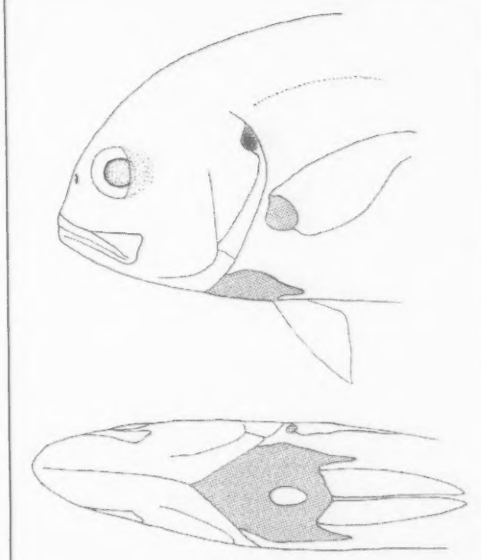


Figure 4

Breast squamation (naked areas shaded) of longfin crevalle jack (*Caranx fischeri*), ANSP 158495, 154 mm FL, Nigeria.

carangid species reveals an almost complete continuum of dentition types that in some cases does not agree with traditional generic assignments. In all members of the *C. hippos* complex the upper jaw has an outer row of strong canines (widely spaced in adults) and an inner band of small villiform teeth that is widest anteriorly. The lower jaw has a single row of strong conical teeth that are smaller anteriorly, and one or two pairs of noticeably enlarged inner symphyseal canines. Enlarged symphyseal dentary canines are absent in the following species of *Caranx*: *C. crysos*, *C. caballus* Günther, *C. melampygus* Cuvier, *C. papuensis*, and *C. senegallus* Cuvier. Gill (1862) proposed the genus *Paratractus* for *Caranx pisquetus* Cuvier, a junior synonym of *C. crysos*, primarily because of the absence of symphyseal canines.

Some recent authors follow Randall (1996) in assigning several common Atlantic carangids to the genus *Carangoides* Bleeker, but we maintain traditional usage for reasons given by Smith-Vaniz et al. (1999, p. 237).

Hyperostosis in *Caranx* species

Hyperostosis appears to have been an integral part of the evolutionary history of the *Caranx hippos* complex, but the pattern of expression is surprisingly different in each species (Table 1). Hyperostosis involves the expansion or swelling of certain bones into globose, gall-like structures characterized by cellular bone foci and bone-resorbing osteoclasts.

In most carangids the condition is usually apparent only in relatively large individuals (but can be detected histologically in smaller individuals) and the onset in different bone foci is typically sequential rather than simultaneous. A large number and size range of individuals of each species usually must be examined before the ontogenetic pattern can be precisely determined. Although Smith-Vaniz et al. (1995) were unable to determine the functional significance of hyperostosis, they found no histological evidence of hyperostosis as a pathologic condition and concluded that the intraspecific predictability and site-specificity of hyperostosis in a taxonomically diverse group of marine fishes was indicative of genetic control.

A detailed description of hyperostosis in *Caranx* is beyond the scope of this article, but to appreciate the context of its site-specificity and distribution in the *C. hippos* complex we briefly discuss its known occurrence in the genus. We found no evidence of hyperostosis in adults of six species: *C. heberi*, *C. ignobilis*, *C. lugubris*

Table 1

Comparison of hyperostosis in the *Caranx hippos* species complex. Sizes are minimum fork length at which hyperostosis is usually developed in all individuals.

Hyperostotic bones	*C. fischeri* (E. Atlantic)	*C. hippos* (E. Atlantic)	*C. hippos* (W. Atlantic)	*C. caninus* (E. Pacific)
Posttemporal	yes >20 cm, Fig. 5	none	none	none
Cleithrum	none	well-developed, >35 cm Fig. 10	well-developed, >35 cm Figs. 9, B–C	none
Neural spines	none	slight, 56 cm	well-developed, >40 cm Figs. 9, B–C, 13	none
Pleural ribs	well-developed >34 cm (usually ribs 5–7), Figs. 5, B–C	slight, 56 cm (ribs 6–8)	well-developed, >38 cm (usually ribs 6–8), Figs. 9, B–C	none or 5th rib only, Fig. 14A (in 6 of 16 spec. >34cm)
Pelvic girdle	none	well-developed, 56 cm	well-developed, >50 cm	well-developed, >45 cm
1st pterygiophore of dorsal fin	none Figs. 5, 11	slight, Figs. 10, 11, 12A	well-developed, Figs. 9, 11, 12B	well-developed, Figs. 11, 14
1st pterygiophore of anal fin	none not convex anteriorly convex anteriorly,	none not convex anteriorly	none not convex anteriorly, Fig. 15	well-developed, >40 cm Figs. 14, 15

Poey, *C. melampygus*, *C. papuensis*, and *C. tille* Cuvier. In addition to *C. fischeri*, hyperostotic posttemporal bones are present in large individuals of the blue runner (*C. crysos*) and green jack (*C. caballus*) allopatric species that are possibly conspecific. *Caranx hippos* is exceptional in that the neural spines of at least vertebrae 6–12 are hyperostotic in large adults. The ventral end of the cleithrum is hyperossified in large *C. hippos*, *C. latus*, and *C. sexfasciatus*, but the shape of the hyperossifcation is noticeably different (wider and shorter) in the latter two species, which also differ from *C. hippos* in having two separate regions of hyperostosis on the cleithrum. The pelvic bones are hyperossified only in *C. hippos* and *C. caninus*. In large adults of *C. caninus* and western Atlantic *C. hippos* the first pterygiophore of the spinous dorsal fin becomes so enlarged that it resembles an oblong swollen fruit; but see discussion of geographic variation associated with hyperostosis of this pterygiophore in *C. hippos* species account. Even in small individuals of both species (where no pterygiophore swelling is evident), this bone is noticeably wider in lateral profile than in similar size individuals of *C. fischeri*, a species that never develops hyperostosis in this pterygiophore. The only site of hyperostosis in *C. senegallus* (largest specimen examined was 30 cm FL) is the posterior part of the supraoccipital crest. Hyperostosis is extensive in *C. bucculentus* Alleyne and Macleay and includes the entire supraoccipital crest, first supraneural, first pterygiophore of the dorsal and anal fins, and a pair of patches on the caudal fin near its base. The ribs on precaudal vertebrae 5–7 (*C. fischeri*) or 6–8 (*C. hippos*) exhibit extensive hyperostosis in relatively large individuals, but *C. fischeri* differs in that only the distal half of each rib is hyperossified. The only apparent contradiction to the consistent site specificity of hyperostosis in the *C. hippos* group is the pattern of occurrence seen on ribs of *C. caninus*. Ribs of the fifth precaudal vertebra appear "normal" in nine specimens (359–643 mm FL), are strongly and uniquely hyperostotic in six others (335–431 mm FL), and in SIO 65–176A (670 mm FL) there is a slight but noticeable swelling only in the middle part of the rib. Even more unexpectedly, in two of six individuals only one rib of these bilaterally paired structures was strongly hyperostotic and its counterpart rib exhibited no hyperostosis.

Caranx carangopsis Steindachner, described from mid-Miocene deposits near Vienna, Austria, also deserves mention. Heckel (1852) recognized the distinctiveness of this fossil species and gave it a scientific name, but the subsequent description was prepared entirely by Steindachner (1859) who must be credited as author of the species. The original description is based on an incomplete series of disarticulated bones, some of which are clearly hyperostotic, from several individuals estimated to have been about 0.9 meters in length. The scientific name refers to the presumed close relationship of this fossil species to *C. carangus* (=*C. hippos*)—a relationship based, in part, on the occurrence of hyperostotic bones (including the ribs, some of the vertebrae, and the first dorsal-fin pterygiophore) in both species. The text descriptions and illustrations of the massively swollen first pterygiophore and pleural ribs of *C. carangopsis* agree reasonably well with those of western Atlantic *C. hippos*, but do not resemble that characteristic of eastern Atlantic *C. hippos*. Steindachner's (1859) accurate description (footnote on p. 690) of the swollen neural spines of the vertebrae in a 1220 mm TL *C. carangus* (=*C. hippos*) also contrasts sharply with his illustrations (pl. 7, Figs. 1–3) of the very differ-

ent thickened vertebrae of *C. carangopsis*. These fossil vertebrae are similar to those of hyperostotic *Trachurus trachurus* Linnaeus (see Desse et al., 1981), suggesting that the original description of *C. carangopsis* is likely based on material (deposited at NMW) from two carangid genera.

Biology, fisheries, fish size, and edibility

Remarkably little information has been published on the biology of members of the *Caranx hippos* complex. Both Kwei (1978) and McBride and McKown (2000) discussed the importance of estuaries as nurseries for juvenile *C. hippos*, and such importance undoubtedly also applies to the other species. The former work is a comprehensive reference on the biology and fisheries of the "crevalle jack" in West Africa; unfortunately no photographs or meristic data were included that can be used to confirm the identification of species. *Caranx hippos* may well have been the most abundant species in the study, but *C. fischeri* is also very common in the region and almost certainly was included in some of the samples.

Noting the occurrence of smallest juveniles in his study, Berry (1959) stated that off the southeastern Atlantic coast of North America spawning probably occurred offshore from March to September. Kwei (1978) reported juveniles present in Ghanaian lagoons (Keta region) during every month of the year and re-entering the sea at sizes ≥12 cm FL. Large shoals of *Caranx* entered Ghanaian inshore waters from September to December, spawning appeared to be protracted, and peak spawning activity (determined from limited data) occurred from October to late January. Low frequency of ripe fish from inshore waters indicated that spawning occurred offshore. Thompson and Munro (1983) reported collecting seven "ripe" *C. hippos*, four males and three females, in the vicinity of Jamaica. The smallest ripe males and females were 55 and 66 cm FL, respectively. Adults were found occasionally in reef habitats and reproductively active fish were taken in May, July, and November. Hildebrand (1939) recorded seven females (67–98 cm TL) with large or developing roe and 11 males (69–88 cm TL), most with developed testes, during 20–24 February 1935 from Gatun Locks, Panama Canal. McBride and KcKown (2000) reported young-of-the-year *C. hippos*, <4.0 cm FL, present in subtropical estuaries (North Carolina to Florida) from June to November and discussed literature indicating that 9°C was likely the lower lethal temperature for the species. Franke and Acero (1993) suggested that *C. caninus* spawns throughout the year, peaking in January–February and August. Examining 96 specimens, they reported a 1:1 sex ratio, and the smallest mature males and females were 67 and 65 cm TL, respectively.

All species of the crevalle jack complex are major predators of small schooling fishes in coastal areas. In the western Atlantic (Florida, Louisiana, and Texas), Saloman and Naughton (1984) reported that small jacks fed primarily on clupeids and larger fish fed usually on clupeids, carangids, and sparids, but penaenoid shrimps, crabs, and other invertebrates were also consumed. Clupeids (*Sardinella* and *Engraulis*) were also the dominant prey of *C. hippos* in the Gulf of Guinea, and juvenile shrimps contributed 50–80% of the diet of juvenile fish during the dry season (Kwei, 1978).

Most commercial landings of crevalle jack in the western Atlantic are from Florida, and annual catches of 221 to 320 t (metric tons) were recorded during 2000–2004 (NMFS[2]). In the eastern Atlantic, where data for *C. hippos* and *C. fisheri* are combined under "crevalle jack," commercial landings are reported only from Angola, Ghana, São Tome, and Principe, and for years 1995–2004 ranged from 2233 to 10,054 t (FAO, 2006). In the Gulf of Guinea, beach seine and set net fisheries for crevalle jack historically supported a large dried or salted fish industry. Okera (1978) reported *C. hippos* (as *C. carangus*) to be one of the dominate pelagic species in the beach seine fishery at Lumley, Sierra Leone, and that 80–100 cm TL fish were most common during September–October. Catches from Ghana in the mid 1950s to early 1960s and from Angola in the 1970s exceeded 15,000 t during some years, but such large catches no longer occur (FAO statistical data *in* Froese and Pauly[3]).

With regard to fighting ability of the crevalle jack, Shipp (1986) stated "there is no tougher game to be had in shallow coastal waters with light tackle than this species." *Caranx hippos* is more important in recreational fisheries in the United States (statistics based only on Atlantic Coast, Gulf of Mexico, excluding Texas and Puerto Rico) and for years 2000–2004 annual catches ranged from 409 to 1030 t (NMFS[2]). Recreational fishing also occurs in West Africa for both *C. hippos* and *C. fisheri* (Schratwieser[4]).

The IGFA All-Tackle world-record *C. hippos*, from Barra do Kwanza, Angola, was caught in December 2000, weighed 26.5 kg (58 lb 6 oz) and was 114 cm FL and 129 cm TL; several other fish almost as large have also been recorded from West Africa. One *C. fischeri* caught at Ozouri Zimbani, Gabon, in January 1989, weighed 20.9 kg, and was approximately 100 cm FL and 127 cm TL. An even larger one (see Fig. 8C), released without being measured or weighed (est. weight 26 kg) was caught in Loango National Park (Iguela Lagoon mouth), Gabon, in December 2005. The IGFA All-Tackle world-record *C. caninus* was caught at Playa Zancudo, Costa Rica, in March 1997, weighed 19.7 kg, and was 101.6 cm TL.

Crevalle jacks are strong fast-swimming predators with large quantities of red muscle and consequently

---

[2] NMFS (National Marine Fisheries Service). 2006. Fisheries Statistics Division. Website: http://www.st.nmfs.gov/st1/ (accessed August 2006).

[3] Froese, R., and D. Pauly, eds. FishBase world wide web electronic publication. Website: http://www.fishbase.org version (07/2006) (accessed August 2006).

[4] Schratwieser, J. 2006. Personal commun. International Game Fish Association, 300 Gulf Stream Way, Dania Beach, Florida, 33004.

their flesh is generally considered coarse and relatively unpalatable. Small individuals are more flavorful and bleeding immediately after capture is recommended. According to Shipp (1986), some of the better seafood cooks make delectable marinated specialties using *C. hippos*.

Caranx fischeri, new species
Longfin crevalle jack
(Figs. 1A, 4–7, 8, A–C, 11; Tables 1–4)

Caranx hippos (not of Linnaeus): Clark, 1915:385 (listed; Ascension Island); Fowler, 1919:254 (brief description; not distinct from American examples); Norman and Irvine, 1947:140, Fig. 65 (biology; artisanal fishery; Ghana); Tortonese, 1952:302, Figs. 11–12 (description; Mediterranean specimens and records); Franca, 1954:24, pl. 3 Figs. 2–3 (description; Luanda, Angola); Poll, 1954:131, Fig. 37, pl. 4, Figs. 1 and 3 (description); Cadenat, 1960:1392 (compared with "*C. carangus*"=*C. hippos*); Cadenat, 1961:240 (listed); Bauchot and Blanc, 1963:43, Fig. 2c (in part, composite description, also includes *C. hippos*; distribution); Daget and Stauch, 1968:40 (listed; Congo);Williams, 1968:252 (maximum reported size 75 cm); Blache et al., 1970:313, Fig. 818 (identification key; distinguished from "*C. carangus*"=*C. hippos*); Daget and Iltis, 1965:238, Fig. 152 (description; Ivory Coast); Tortonese, 1975:156, Fig. 64 (description; Mediterranean records, after Tortonese, 1952); Okera, 1978:85 (beach seine fishery, occasionally taken with "*C. carangus*"=*C. hippos*; Sierra Leone); Smith-Vaniz and Berry, 1981: unpaginated; Fig. (in part, composite description; distribution); Bianchi, 1986:49, Fig., color pl. II, Fig. 10 (habitat; biology; fisheries utilization; Angola); Smith-Vaniz, 1986:824, Fig. (in part, composite diagnosis; habitat; distribution); Bellemans et al., 1988:46, Fig., color pl. 2, Fig. 10 (local names; habitat); Papaconstantinou, 1988:95 (compiled; Greek seas); Edwards and Glass, 1987:1377 (unconfirmed records, St. Helena); Edwards, 1990:97, Fig. 48 (compiled description; unconfirmed occurrence at St. Helena); Smith-Vaniz et al., 1990:732 (in part, composite synonymy; distribution); Afonso et al., 1999:73 (listed; Gulf of Guinea); Bilecenoglu et al., 2002:84 (Aegean and Turkish seas; compiled); Edwards et al., 2003:2238 (J. R. Irvine's Ghanaian specimens).

Caranx carangus (non Bloch): Ehrenbaum, 1915:65 (misidentification, in part, Fig. of *C. hippos* after Goode, 1984; description; Cameroon); Chabanaud and Monod, 1927:18, Fig. 24 (listed, rare; Port Etienne, Mauritania); Collignon et al., 1957:192, Fig. 47 (brief description).

Holotype ANSP 140256 (328 mm FL), Cameroon, Douala, 22 Aug 1978, obtained by P. J. P. Whitehead.

Paratypes One-hundred twenty-eight specimens (33–530 mm FL) from 56 collections. SENEGAL: IRSNB 829 (530), Dakar, Madeleine Island, 9 Nov 1949, G. Marlier; MNHN 1978-260 (313), coast of Senegal. GUINEA: ISH 163/62 (227), 9°45′N, 13°55′W, 17 m. SIERRA LEON: ANSP 158497 (237), Freetown, 8°29′24″N, 13°11′30″W, 6 m, hook and line, 9 Feb 1968, RV *Undaunted* Cr. 6801, G. Beardsley; ANSP 158498 (239), 7°07′N, 11°57′30″W, 18–21 m, Guinea Trawling Survey I, RV *La Rafale*, Trans. 12, sta. 1, 13 Nov 1963; BMNH 1928.8.3.14 (164.5), "Sierra Leone," J. Hornell; USNM 279566 (2, 163–203), St. Anne Banana Islands, 15–25 m, Feb 1986, G. Naylor. LIBERIA: USNM 193784 (121), Mesurado River beach, 6°19′N, 10°48′W, 24 May 1952, G. C. Miller; USNM 193790 (148) and USNM 193792 (102), Mesurado River beach, 20 Jun 1952, G. C. Miller; USNM 193779 (2, 148–163), Monrovia, Freeport, 5 May 1953, G. C. Miller. IVORY COAST: MNHN 1978-200 (253). GHANA: BMNH 1930.8.26.49-50 (2, 91–139), Accra, Mar 1930, F. R. Irvine (Irvine 53); BMNH 1938.12.15.48 (114), Volta River, Amedica, May 1938, F. R. Irvine (Irvine 237); BMNH 1939.7.12.12 (271), Prampram, Sep 1938, F. R. Irvine (Irvine 316); CAS-SU 64645 (118), Volta River; CAS-SU 64648 (124), Lower Volta River, Jun–Jul 1963, W. Titiati; CAS-SU 64700 (69), Battor River, 2 Mar 1964, T. R. Roberts; CAS-SU 66674 (41), Volta River at Amedia, 8 Mar 1963, T. R. Roberts; CAS-SU 69861 (2, 35–40), mouth of Volta River at Little Ada, 12 Jan 1963, T. R. Roberts; USNM 373240 (17, 33–52), Volta River at Big Ada, 9 Mar 1960, G. W. Bane; USNM 300660 (113), Tema Nunga, 18 May 1962, G. W. Bane; USNM 373242 (22, 37–52), beach at Tema fishing harbor, 15 Dec 1959, G. W. Bane; USNM 365702 (16, 71–90), Dix Cove Amaful, 25 Jan 1961, G. W. Bane; USNM 373244 (56), Ahiado River W. of Amanful, Takoradi, 4 Feb 1961, Amegah; USNM 368973 (3, 49–88), Ashantee, Beyah River, 27 Nov 1889, W. H. Brown, U.S. Eclipse African Exped. TOGO: ZMH 14575 (155), lagoon near Anecto, "Dr. Liebl," summer 1909. BENIN: MNHN 1967-826 (198), 6°15′N, 2°38′E, 23 m, 27 Jul 1964, A. Crosnier and J. Marteau. NIGERIA: BMNH 1968.11.15.31-32 (2, 85–169), Lagos Lagoon, 1967, S. O. Fagade; ANSP 158495 (3, 154–163), 4°15′N, 6°49′E, 15 m, Guinea Trawling Survey II, RV *Thierry*, trans. 43, sta. 1, 5 Apr 1964; CAS 38373 (135), 6°21′N, 2°54′E, 15 m, Guinea Trawling Survey II, RV *Thierry*, trans. 36, sta. 1, 19 Mar 1964; CAS 38375 (2, 145–160), 4°28′N, 5°07′E, 19 m, Guinea Trawling Survey II, RV *Thierry*, trans. 41, sta. 7, 2 Apr 1964; CAS 38395 (2, 146–150), 5°15′N, 5°09′E, Guinea Trawling Survey II, RV *Thierry*, trans. 40, sta. 1, 30 Mar 1964; ISH 1147/64 (145), 5°09′N, 4°39′W, 20 m; ZMUC P.46362 (450), Bonny River, 22 Feb 1946, "Atlantidae" sta. 111; MNHN 1896-327 (153), Campagne Touree; BMNH 1956.9.6.68 (183), Lagos Tarkwe, F. Williams. CAMEROON: ANSP 140288 (156), Victoria, 23 Aug 1978, FAO; BMNH 1936.12. 29.7 (172), Victoria, Cross River; D. Tovey; CAS-SU 15883 (2, 41–44), Bwanjo, Bwanjo River, 15 Sep 1936, A. I. Good; CAS-SU 15884 (150), Kribi, 25 Oct 1938, A. I. Good; CAS-SU 15885 (171), Kribi, 23 Feb 1940, A. I. Good; CAS-SU 18221 (77), Mbode, 23 Dec 1940, A. I. Good; CAS-SU 18222 (82), Kribi, Kribi River, 24 Sep

1940, A. I. Good; CAS-SU 64900 (70), Kirbi, Kirbi River, 23 Nov 1940, A. I. Good; MNHN 1978-336 (147), Depierre; MNHN 1982-1093 (117), Yabassi, Depierre, 1980. UF 142347 (2, 144–155), 2°28′N, 9°44′E, 15–16 m, Guinea Trawling Survey II, RV *Thierry* Trans. 49, sta. 1, 25 Apr 1968; USNM 304197 (81), S. Korup at coast, Rio del Rey, 10 Mar 1988, G. M. Reid; ZMH 14576 (135), Douala, J. V. Eitzen, 1912–1913. EQUATORIAL GUINEA: ANSP 158493 (4, 173–197), Bioko (Fernando Po) 3°35′N, 9°19′E, 30 m, Guinea Trawling Survey II, RV *Thierry,* trans. 47, sta. 2, 18 Apr 1964; UF 142348 (2, 52–64), Bioko (Fernando Po), fresh water pool on SE end of island, 25 Sep 1959, G. W. Bane. GABON: CAS 38376 (197), 0°21′N9°15′E, 20 m, Guinea Trawling Survey II, RV *Thierry,* trans. 52, sta. 1, 7 May 1964; BMNH 1896.5.5.14 (102), Corisco Island, M.H. Kingsley. CONGO: BMNH 1899.2.20.3 (173), Manyanga; BMNH 1899.11.27.87 (348), Banana; M. Delhez; MRAC 36 (403), Banana, 1896, Lt. E. Wilverth; MRAC 87428 (367), Banana, 1952, Major Marée. ASCENSION ISLAND: BMNH 1927.12.7.49 (358), J. Simpson.

Other material Centro Oceanográfico de Canarias, Tenerife, uncataloged (310), Benin, trawled in 38 m, 28 Jul 2002, FAO; SAIAB 26541 (130), Gulf of Guinea between Cameroon and Bioko; SAIAB 26541 (7, 138–233), Gulf of Guinea; MNHN 1978-235 (317), coast of tropical French Africa.

Diagnosis A member of the *Caranx hippos* complex with the following combination of characters: segmented dorsal-fin rays 21–23 (exceptionally 24); segmented anal-fin rays 17–19, usually 18; posttemporal bones hyperossified in specimens larger than 20 cm FL (Fig. 5); cleithrum, first pterygiophore of dorsal and anal fins, and neural spines of vertebrae relatively slender and never hyperossified; in specimens >20 cm FL, heights of longest dorsal- and anal-fin rays both 0.7–1.3 in head length; in adults, anal-fin lobe white anteriorly and remainder of fin gray to brown.

Description Total range of values given first, followed by values for holotype in parentheses: dorsal-fin rays VIII-I, 21–24 (22); anal-fin rays II-I, 17–19 (18); pectoral-fin rays 18–21 (21); vertebrae 10 precaudal + 14 caudal; curved lateral-line scales 50–73 (69); straight lateral-line scales 0–16 (4); straight lateral-line scutes 24-41 (35); total scales + scutes in straight lateral line 32–47 (39); developed gill rakers 2–7 (3) upper, 14–17 (14) lower, 16–24 (17) total; rudimentary gill rakers 0–4 (4) upper, 0–3 (3) lower, 4–8 (7) total; rudimentary + developed gill rakers 20–25 (24) total.

Posttemporal bones distinctly hyperossified in specimens larger than 20 cm FL (Fig. 5); cleithrum, pelvic bone, first pterygiophore of dorsal and anal fins, and vertebral neural spines not hyperossified, the latter relatively slender; in specimens ≥34 cm FL distal half of pleural ribs of vertebrae 5–7 hyperostotic; anterior dorsal-fin pterygiophore formula S/S-S/2+1/1; supraneurals relatively robust proximally; first anal-fin pterygiophore elongated anteroventrally.

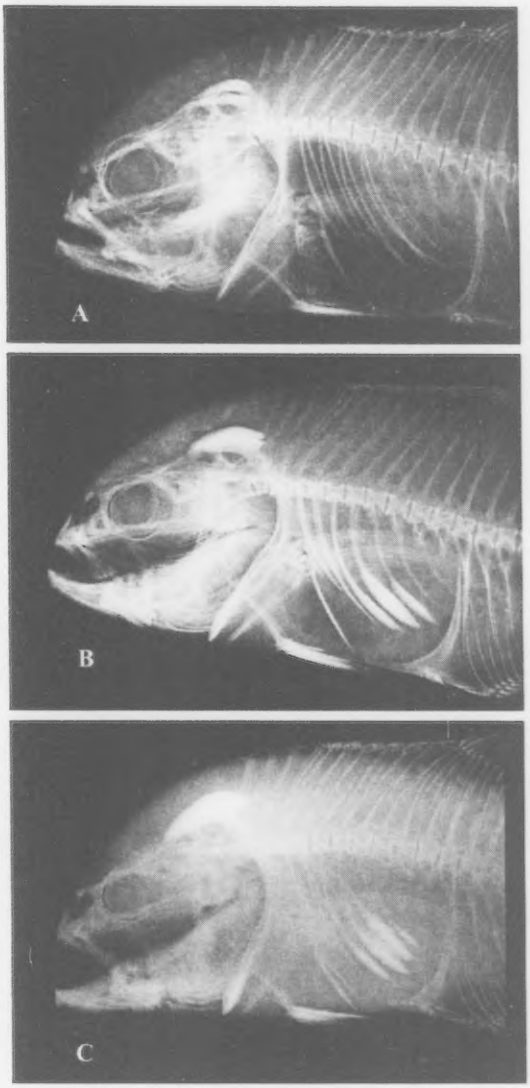


Figure 5

Radiographs of longfin crevalle jack (*Caranx fischeri*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (**A**) BMNH 1939.7.12.12, 271 mm FL, Gold Coast; (**B**) BMNH 1899.11.27.87, 348 mm FL, Congo; (**C**) ZMUZ P.46362, 450 mm FL, Nigeria.

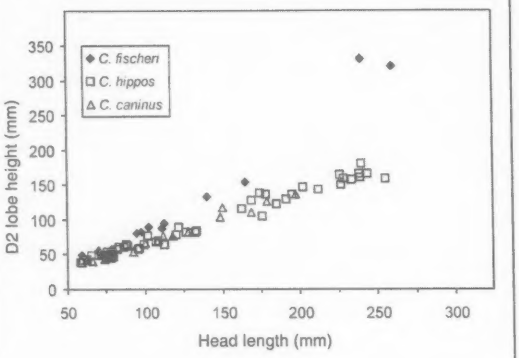


Figure 6

Dorsal-fin lobe height versus head length in members of the crevalle jack (*Caranx hippos*) complex.

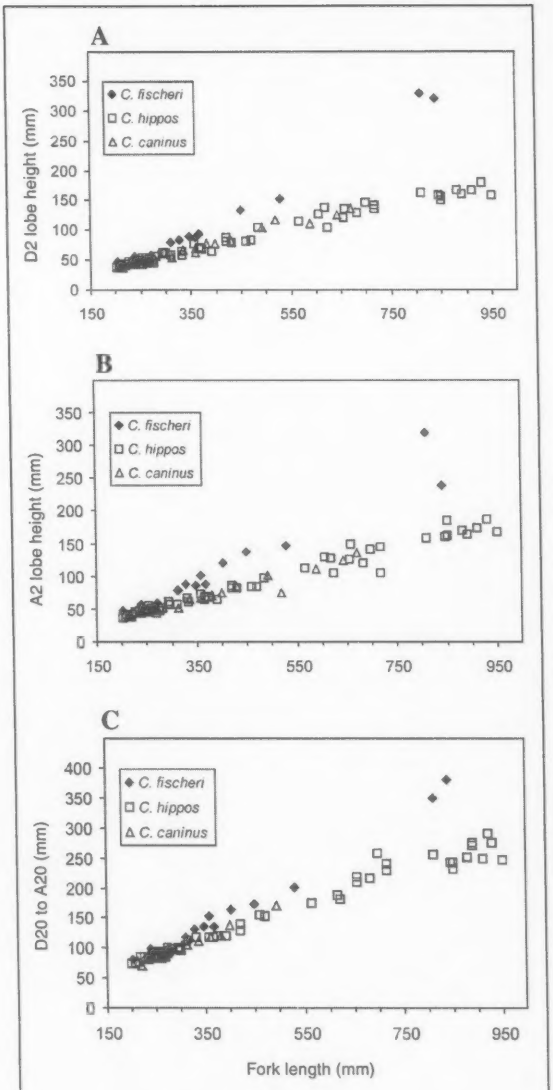


Figure 7

Selected measurements versus fork length (FL) in members of the crevalle jack (*Caranx hippos*) complex: (**A**) dorsal-fin lobe height versus FL; (**B**) anal-fin lobe height versus FL; (**C**) body depth (D2O to A2O) versus FL.

Body robust and compressed; head blunt—upper profile strongly convex, lower profile only slightly curved anteriorly; caudal peduncle slender. Breast naked ventrally to origin of pelvic fins, except for a small oval or oblong patch of scales in front of pelvic fins (Fig. 4); laterally, naked area sometimes extending slightly behind pelvic fins as a narrow wedge and always separated from naked base of pectoral fin by a narrow-to-broad band of scales; maxilla, lacrimal and dorsum of head naked; cheeks, preopercle, and opercle covered with scales; bases of dorsal and anal fins have a narrow scaly sheath anteriorly. Junction of curved and straight parts of lateral line below segmented dorsal-fin rays 5–10 (9); length of curved lateral line 0.93–1.47 (0.97) in straight lateral line. Dorsal fins well separated; first spine of spinous dorsal fin very slender and closely applied to second spine, posterior 1–4 spines partially or completely embedded in large adults; third spine longest and much shorter than height of second dorsal-fin lobe. Height of second dorsal-fin lobe 0.7–1.3 (1.2) in head length; height of anal-fin lobe 0.7–1.3 (1.1) in head length; heights of both fin lobes longer than head in large adults (Figs. 6–7). Pectoral fin of adults long and falcate, 0.8–0.9 (0.8) in head length.

Upper jaw 2.2–2.3 (2.2) in head length, extending to or slightly behind posterior margin of eye; eye diameter 4.0–6.1 (4.3) in head length, and adipose eyelid well-developed, especially posteriorly, in adults. Upper jaw with an outer row of strong canines (widely spaced in adults) and an inner band of small villiform teeth that are widest anteriorly; lower jaw with a single row of strong conical teeth that are smaller anteriorly and one (occasionally two) pair of noticeably enlarged inner symphyseal canines. Vomerine tooth patch triangular-shaped, without a median posterior extension, and sparsely covered with small teeth.

Measurements of 14 paratypes, 203–530 mm, and the holotype as percentages of FL: snout to D1O 40.7–43.9 (41.6); snout to D2O 55.7–59.8 (57.0); snout to P2O 29.8–34.3 (30.2); snout to A2O 55.5–60.2 (58.8); D1O to P2O 33.4–39.0 (35.5); D2O to A2O 35.3–42.6 (40.2); D2 base 31.2–34.1 (32.2); A2 base 28.4–32.5 (28.7); curved lateral-line length 27.6–36.0 (34.3); straight lateral-line length 32.1–43.8 (33.3); height of dorsal-fin lobe 21.6–29.6 (25.3); height of anal-fin lobe 22.7–30.6 (26.8); pelvic-fin length 13.6–15.7 (13.9); pectoral-fin length 33.7–38.7

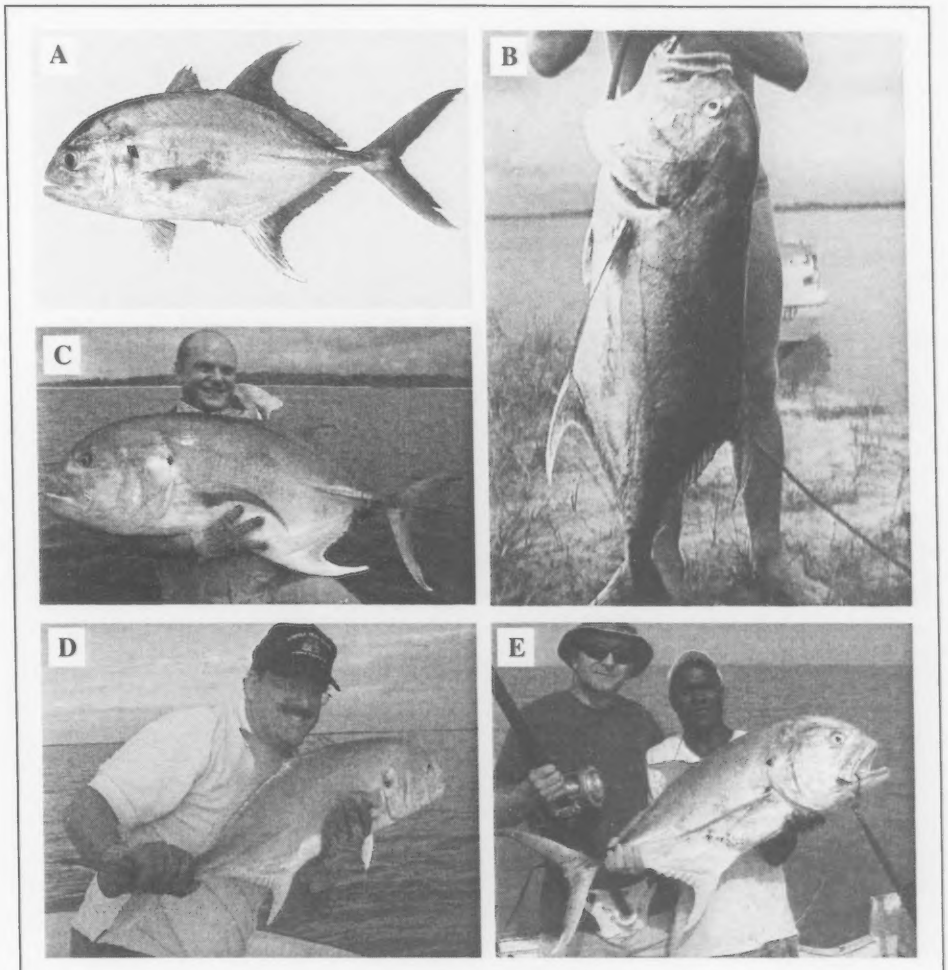


Figure 8

Longfin crevalle jack (*Caranx fischeri*) (**A–C**) and crevalle jack (*Caranx hippos*) (**D** and **E**): (A) 31 cm FL, Benin, FAO; (B) 20.9 kg and ca. 100 cm FL, Gabon, IGFA; (C) ca. 26 kg, Gabon, A. Choinier; (D) Florida Bay, Gulf of Mexico, J. P. Reid; E) Angola, IGFA.

(36.4); head length 29.0–31.6 (29.9). As percentages of head length: postorbital head length 49.5–57.4 (50.5); snout length 24.4–28.4 (26.1); eye diameter 16.4–25.2 (23.1); upper jaw length 43.1–46.3 (45.2).

Fresh coloration of adults (Fig. 8, A–C) olive to greenish-blue dorsally, changing to silvery white on lower sides and ventrally; prominent black spot, approximately diameter of pupil, posteriorly on opercle at level of eye; an oval black spot on lower pectoral-fin rays and in upper axil of pectoral fins; dorsal fin dark brown; anal-fin lobe mostly white, especially anteriorly, and remainder of fin brownish-yellow; pelvic fins white and caudal fin brownish-yellow.

In preserved adults, the dark spot on the opercle and dark blotch on lower pectoral-fin rays are readily apparent, the latter on rays 6 or 7 to 14–16 (counting ventrally). The relatively pale anterior of the anal-fin lobe in comparison to the remainder of the fin is also evident. Small juveniles have five dusky bands on body; lack the dark blotch on the pectoral fin, have a heavily pigmented spinous dorsal fin and the dorsal-fin lobe is dark distally. Two juveniles, 35–40 mm FL (CAS-SU 69861) collected near the mouth of the Volta River, Ghana, had the identical pigmentation of 28 specimens of *C. hippos* (CAS-SU 64646) taken in the same collection, including some in the same size range. Berry

Table 2

Frequency distributions of segmented dorsal- and anal-fin rays in the *Caranx hippos* species complex.

	Dorsal-fin rays								Anal-fin rays					
Species	19	20	21	22	23	24	*n*	$\bar{x}$	16	17	18	19	*n*	$\bar{x}$
C. fischeri			31	93	10	1	135	21.9		17	104	14	135	18.0
C. hippos (E. Atlantic)	28	35					63	19.6	54	9			63	16.1
C. hippos (W. Atlantic)	18	130	13				161	20.0	103	58			161	16.4
C. caninus	28	66	6				100	19.8	69	31			100	16.3

	Dorsal + anal rays											Pectoral-fin rays			
Species	35	36	37	38	39	40	41	42	43	*n*	$\bar{x}$	18	19	20	21
C. fischeri				15	18	83	13	5	1	135	39.8	1	12	57	12
C. hippos (E. Atlantic)	26	30	7							63	35.7	1	18	21	1
C. hippos (W. Atlantic)	22	79	51	9						161	36.3	3	68	50	2
C. caninus	25	47	22	6						100	36.1		15	38	8

(1959) included excellent illustrations of young *C. hippos* and *C. latus*. As both he and Laroche et al. (2006) discussed, small juveniles of these two species can not be distinguished solely by pigmentation. Thus, as might be expected, juveniles of *C. fischeri* and *hippos* also apparently cannot be distinguished by color pattern.

Comparisons and relationships The unique pigmentation of the pectoral fin in adults, pattern of breast squamation (a relatively small number of *C. hippos* and *C. caninus* are atypical in having the naked area of the breast continue without interruption to the pectoral-fin base), and the relatively large symphyseal dentary canines, which are shared by all members of the *hippos* complex, indicate their common ancestry. Of the three extant species, *C. fischeri* is readily distinguished by typically having more dorsal- and anal-fin rays (Table 2), and in specimens >20 cm FL the anterior dorsal- and anal-fin rays are relatively longer, and the body is deeper. The pattern of bones that exhibit hyperostosis is markedly different from that of the other species (Table 1), in neither of which is the posttemporal bone hyperossified. The anal-fin lobe is white anteriorly in adults of *C. fischeri*, in contrast to the uniformly lemon yellow lobe of *C. hippos*. Adults of *C. hippos* also differ in having the underside of the caudal peduncle bright yellow.

The presence of hyperostosis in a particular bone is presumed to be a derived condition (and conversely, the absence of hyperostosis is uninformative). On the basis of shared character states 5–6 (Table 1), *C. hippos* and *C. caninus* are considered to be sister species, and the geologically recent (~3.1 mya) rise of the Panamanian Isthmus was the likely vicariant event leading to the isolation and subsequent speciation of *C. caninus*. The common ancestor of *C. fischeri* and *C. hippos-caninus* presumably originated in the proto-Atlantic Ocean; and the sympatric occurrence of both *C. fischeri* and *C. hippos* in the eastern Atlantic is likely indicative of an earlier phylogenetic origin.

Distribution African coast from Mauritania south at least to Moçamedes, southern Angola (Franca, 1954), and at least historically it was present in the Mediterranean Sea (Fig. 2). The collection of an adult *C. fischeri* from Ascension Island indicates at least the occasional vagrant occurrence at insular localities. Unconfirmed historical reports of *C. hippos* from both Ascension (Clark, 1915) and St. Helena (Edwards, 1990) are likely based on misidentifications, possibly of *C. fischeri*.

Tortonese (1952) discussed historical Mediterranean specimens dating from the 1890s in the Giglioli Collection and Genova Museum and he identified these specimens as *Caranx hippos*. Our efforts to locate these or recent Mediterranean specimens of *C. hippos* have been unsuccessful (see Tortonese, 1973, for status of historical fish collections in Italy). Data that Tortonese (1952) provided for two of his five specimens, as well as an accompanying photograph of one of them, confirm their identification as *C. fischeri*. We assume that all five specimens were conspecific, and all Tortonese's Mediterranean distributional records are plotted in Figure 2. Papaconstantinou (1988) and Bilecenoglu et al. (2002) cited a few additional unconfirmed literature records of *C. hippos* from the Mediterranean, which we presume were also based on misidentifications of *C. fischeri*; these records are not shown on the distribution map (Fig. 2). See discussion of probable erroneous recent photographic record of *C. hippos* from the Mediterranean in the following species account.

This species is often found in brackish water, sometimes ascending rivers. The paratype series includes collections, mostly of juveniles, from three different river drainages. In their account of *C. hippos*, Norman and Irvine (1947) quoted a secondary source as report-

ing that local fishermen say that *Afãfã* fish (probably *C. fischeri*) swim far up rivers to spawn.

Etymology We take great pleasure in naming this new species *Caranx fischeri* in honor of our friend and colleague Dr. Walter Fischer (retired) for his vision and dedication in initiating the Species Identification and Data Programme of the Food and Agriculture Organization of the United Nations (Fischer, 1989). In numerous ways this program has been an invaluable resource for marine fisheries biologists and ichthyologists generally.

Caranx hippos (Linnaeus, 1766)
Crevalle jack
(Figs. 1B, 3, 6–7, 8, D–E, 9–13, 15; Tables 1–4)

Scomber hippos Linnaeus, 1766:494 (original description; Carolina; putative holotype Linn. Soc. Lond. 130 [Garden no. 16]); Wheeler, 1985:55 (type status).

Scomber carangus Bloch, 1793:69, pl. 340 (original description; Antilles; syntype ZMB 1542).

Caranx erythrurus Lacépède, 1801:58, 68 (no locality stated; based on *Caranx hippos* Linnaeus and other sources).

Caranx carangua Lacépède, 1801:59, 74 (original description; Martinique, West Indies; no type, based on a drawing by Plumier).

Caranx antilliarum Bennett, 1840:282 (unnecessary replacement name for *Scomber carangus* Bloch 1793).

Caranx defensor DeKay, 1842:120, pl. 24, Fig. 72 (original description; New York; type whereabouts unknown).

Carangus esculentus Girard, 1858:168 (name only); Girard, 1859:23, pl. 11, Figs. 1–3 (description; Brazos Santiago, Texas; apparently an unnecessary replacement name for *Scomber carangus* Bloch to avoid "Strickland tautonymy" when Girard provided the new genus name *Carangus*).

Caranx hippos: Goode, 1884:323, pl. 99 (biology, edibility, distribution); Devincenzi, 1924:215, pl. 232, Fig. 1 (description; Rio de la Plata, Uruguay); Hildebrand, 1939:26 (sexual maturity; Panama Canal); Ginsburg, 1952:93, pl. 5, Fig. C (synonymy; description; distribution; Gulf of Mexico); Berry, 1959:503, Figs. 81–85 (juvenile description); Postel, 1959:157 (listed; Mauritania); Bauchot and Blanc, 1963:43 (composite description, also includes *C. fischeri*; distribution); Vergara, 1972 (osteology and relationships of Cuban *Caranx* spp.); Menezes and Figueiredo, 1980:4, Fig. 4 (brief description; Brazil); Smith-Vaniz and Berry, 1981:unpaginated (in part; composite description; distribution); Uyeno et al., 1983:332, color photo (description, Suriname); Shipp, 1986:118, Fig. 133 (habits; edibility; Gulf of Mexico); Scott and Scott, 1988:376 (Canadian occurrence); Smith-Vaniz et al., 1990:732 (composite synonymy; distribution); Cervigón, 1993:63, Figs. 24–25 (description; distribution; Venezuela); Randall, 1996:142, Fig. 173 (brief description; Caribbean); Murdy et al., 1997:165, Fig. 151 (description distribution; ecology; Chesapeake Bay); Debelius, 1997:159, unnumbered color Fig. (Balearic Islands, Spain; locality probably erroneous); Smith-Vaniz et al., 1999:238 (erroneous occurrence records; Bermuda); McBride and McKown, 2000:528 (seasonal dispersal patterns of juveniles between subtropical and temperate habitats; east coast of North America); Brito et al., 2002:220 (misidentification of *C. latus*; Canary Islands); Klein-MacPhee, 2002:415, Fig. 222 (description; early life history; Gulf of Maine); Laroche et al., 2006:1462, Figs. (early stages; early postflexion larvae indistinguishable from *C. latus*).

Carangus hippos: Jordan and Evermann. 1902:306, unnumbered photograph (color description; "everywhere a food-fish of considerable importance").

Caranx hippos tropicus Nichols, 1920:45 (original description; Para, Brazil; holotype AMNH 3889).

Caranx africanus (not of Steindachner): Poll, 1954: pl. 4, Fig. 4 (misidentification; Banana, Congo).

Caranx carangus: Cuvier and Valenciennes, 1833:91, pl. 57, Fig. 2 (description); Duméril, 1861:262 (listed; Gorée); Steindachner, 1870:704 (Senegal); Peters, 1877:836 (listed; Congo); Pellegrin, 1907:90, Fig. 7 (Dakar); Monod, 1927:699, Figs. 16–22B (Cameroon); Cadenat, 1950:171, Fig. 103 (Senegal); Cadenat, 1960:1392 (compared with "*C. hippos*"=*C. fischeri*; Ghana and Nigeria); Williams, 1968:252 (maximum reported size 120 cm); Blache et al., 1970:313, Fig. 819 (identification key; distinguished from "*C. hippos*"=*C. fischeri*); Okera, 1978:84 (abundance in beach seine fishery; Sierra Leone).

Diagnosis This species is a member of the *Caranx hippos* complex and has the following combination of characters: segmented dorsal-fin rays 19–21; segmented anal-fin rays 16 or 17; posttemporal bones never hyperossified; cleithra hyperossified distally in adults ≥35 cm FL (Figs. 9, 10); first pterygiophore of dorsal fin (Figs. 11, 12) and neural spines of some vertebrae (Fig. 13) noticeably (western Atlantic) or slightly to moderately (eastern Atlantic) hyperossfied in adults ≥50 cm FL; first pterygiophore of anal fin not hyperossified in large adults; pleural ribs 6–8 hyperossified in large adults; in specimens >20 cm FL, heights of longest dorsal- and anal-fin rays 1.3–2.1 and 1.2–2.0, respectively, in head length; anal-fin lobe and underside of caudal peduncle bright yellow in adults.

Remarks Nichols and Roemhild (1946) gave frequency counts of dorsal- and anal-fin rays for 42 specimens of *C. hippos* from the western Atlantic Ocean. Their counts of 15 anal soft rays (3 specimens) and 18 dorsal soft rays (2 specimens) were not duplicated (see Table 2) in our material that was based on a total of 161 western Atlantic and 63 eastern Atlantic specimens. Because Berry (1959, Table 21) recorded the same range of soft rays (based on 132 western Atlantic *C. hippos*) that we also recorded, we conclude that the outlier counts given in the earlier study are erroneous.

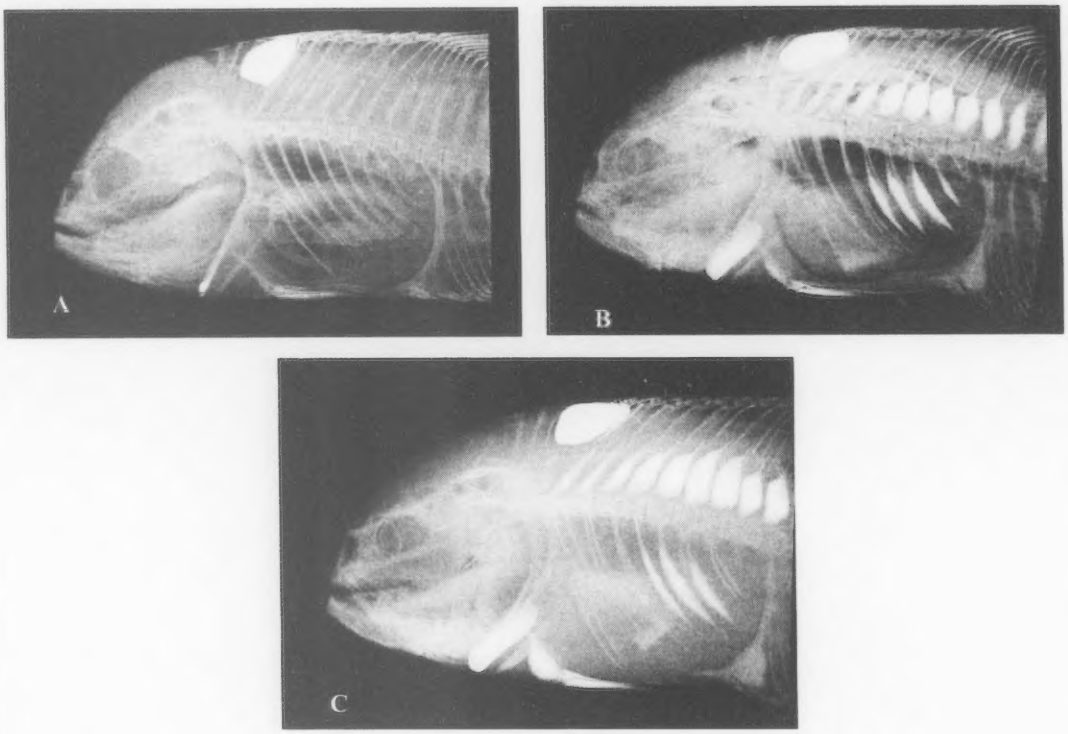


Figure 9

Radiographs of crevalle jack (*Caranx hippos*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (**A**) AMNH 58046, 274 mm FL, Brazil; (**B**) USNM 132964, 400 mm FL, Cuba; (**C**) USNM 114618, 557 mm FL, Guatemala.

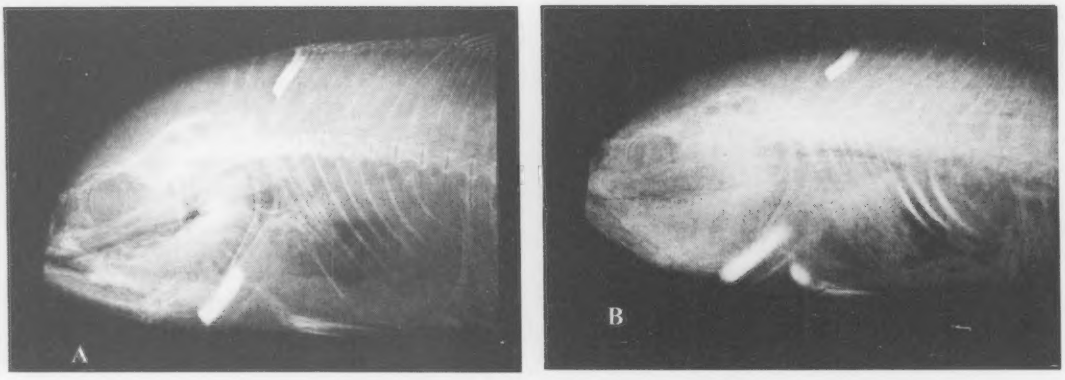


Figure 10

Radiographs of crevalle jack (*Caranx hippos*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (**A**) MNHN 1978-216, 331 mm FL, Mauritania; (**B**) ZMUC 25, 565 mm FL, Senegal.

Comparisons Although long confused with *Caranx fischeri*, as discussed under "Comparisons and relationships" in the account of that species, *C. hippos* is easily distinguished. However, *C. hippos* and *C. caninus* are so similar externally that many authors considered them to be taxonomically identical or only subspecifically distinct. They have broadly overlapping mensural (Figs. 6–7) and meristic values (Tables 2–4), but the pattern of hyperostosis (Table 1) is surprisingly different in the two species. They differ in four character states (Table 1, characters 2–4, 6) and share three others (Table 1, characters 5–6), although even in one of these (Table 1, character 5), the relative degree of hyperostosis is different (Fig. 11), namely the expansion of the first dorsal-fin pterygiophore being more pronounced in *C. caninus*. The color of the anal fin of a living fish is lemon yellow in *C. hippos* and is either uniformly white or brownish-orange in *C. caninus*. The underside of the caudal peduncle in adults of *C. hippos* is mostly yellow, a trait that *C. Caninus* lacks.

Distribution This species is found on both sides of the Atlantic Ocean but is largely restricted to continental shelf areas (Fig. 2). In the western Atlantic it is found from Nova Scotia only as rare waifs (Scott and Scott, 1998) to Rio de la Plata, Uruguay (Devincenzi, 1924), but is absent from Bermuda (Smith-Vaniz et al., 1999) and most of the Lesser Antilles. Confirmed insular locality records based on museum specimens include those for Jamaica and the Bahamas (Andros Island), and we have photographic documentation for the Virgin Islands (St. Thomas) near the southern end of the shallow Puerto Rico shelf, where the species is relatively common. *Caranx hippos* is a regular summer visitor as far north as Woods Hole, Massachusetts (Klein-MacPhee, 2002), and young-of-the-year inhabit temperate estuaries of New York and New Jersey from July to November. McBride and McKown (2000) presented data indicating that these juveniles are spawned in subtropical latitudes and, aided by the Gulf Stream, disperse northward to coastal nurseries. Although the species is incapable of surviving the winter north of Cape Hatteras, growth rates and seasonal changes in distribution of this species indicate that some individuals successfully migrate southward to suitable over-wintering habitat and retain their potential contribution to the spawning population.

In the eastern Atlantic *C. hippos* is known from Mauritania to Angola, but historical records for the Mediterranean Sea (Tortonese, 1952, 1975) are based on misidentifications of *C. fischeri*, as presumably are additional unconfirmed records cited by Papaconstantinou (1988) and Bilecenoglu et al. (2002). The photograph (Debelius, 1997, p. 159) of a large school of adult *Caranx*, identified in the caption as *C. hippos* and stated to have been taken at the Balearic Islands, Spain, may have been a substitution and this locality record for the species could not be confirmed (Debelius[5]). Reports of *C. hippos* from the Canary Islands are based on misidentifications of *C. latus*; and records of the species from the Azores (Arruda, 1997), Cape Verde Islands (Osório, 1911), and St. Helena (Melliss, 1875; Edwards and Glass, 1987; Edwards, 1990) are unreliable and can not been confirmed.

Adults are found inshore and frequently in upstream brackish waters (Klein-MacPhee, 2002) but are most common in salinities higher than 30 ppt (Gunter, 1945). Juveniles appear to use estuaries as nurseries in both temperate and tropical areas. Most reports of the species from freshwater are unreliable because of previous confusion with *C. fischeri* or are misleading (Herald and Strickland, 1949) because Homossassa Springs, Florida, has high alkalinity from the ionic composition of bicarbonate spring effluents. Gunter (1945) recorded juveniles and adults from Texas in salinities from 4.8 to 36.4 ppt. Smith (1985) reported that crevalle jacks are common summer residents in the Lower Hudson River, New York, and "in 1982 they were especially abundant as far upstream as River Mile 68 in early October and were still present at River Mile 66 in early November." McBride and McKown (2000) observed individuals in the Hudson River during July–October 1986–1993 at the freshwater interface (about 1 ppt), about 90–100 km inland.

Geographic variation Juveniles and adults of *C. hippos* from opposite sides of the Atlantic Ocean are virtually identical externally, including life coloration (Fig. 8, D–E), but differ notably in relative development of hyperostosis of the first pterygiophore of the dorsal fin. This bone is much less robust in adults of eastern Atlantic *C. hippos* (Figs. 11, 12). There is some variation in relative development of this pterygiophore in large western Atlantic specimens, but in all those we have examined (including a number of partially articulated skeletons at the AMNH not listed below) it is dorsolaterally expanded in marked contrast to the slender profile of the bone in eastern Atlantic specimens (Fig. 12). The basal halves of the neural spines of some of the anterior vertebrae (usually vertebrae 5–12) are also consistently and strongly expanded (Fig. 9, B–C) in large adults from the western Atlantic. The neural spines are only slightly hyperossified in a 56-cm-FL specimen (Figs. 10B, 13) from Senegal. They were more expanded (although much less so than in similar-size western Atlantic specimens) in a 90-cm specimen from Angola that had been partially dissected and photographed at our request so that we could ascertain the condition of the neural spines.

Caranx hippos has an essentially continental distribution (there are no confirmed records from any oceanic island) and populations on opposite sides of the Atlantic presumably are isolated and have little genetic connectivity, thus some geographic differentiation might be expected. *Caranx senegallus* and *C. fischeri* are both eastern Atlantic endemics, but other Atlantic species of *Caranx* with amphi-Atlantic distributions (*C.*

[5] Debelius, H. 2004. Personal commun. IKAN-Underwasserarchiv, Waldschulstrasse 166, 65933, Frankfurt, Germany.

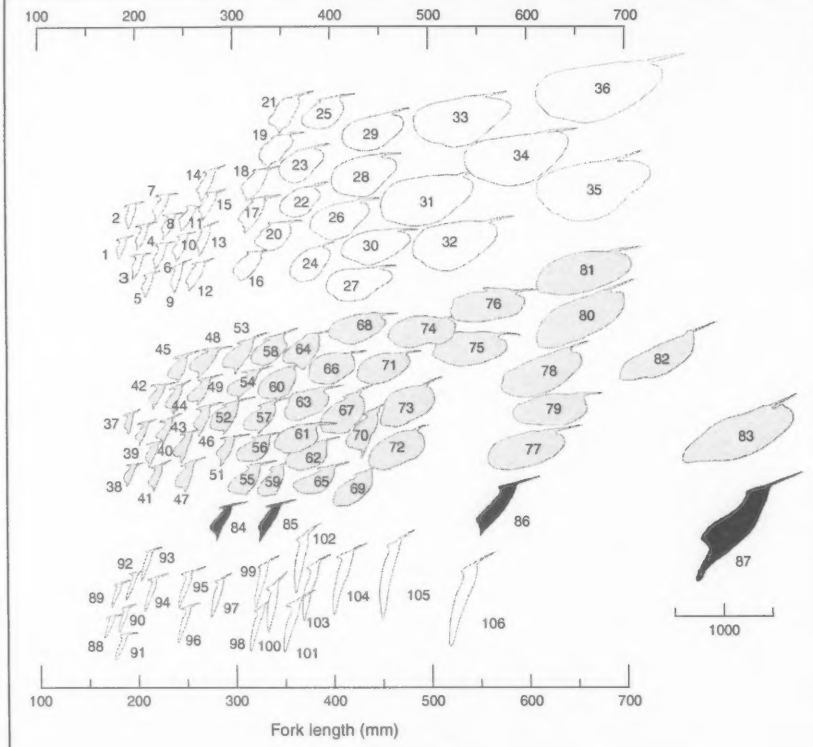


Figure 11

First dorsal-fin pterygiophore in lateral view (anterior of pterygiophore on left). Outlines were traced from radiographs plotted against fork length of Pacific crevalle jack (*Caranx caninus*) (pterygiophores numbers 1–36), crevalle jack (*C. hippos*) (37–83, western Atlantic, 84–87 eastern Atlantic, in black), and longfin crevalle jack (*C. fischeri*) (88–106). Numbers correspond to those given in Appendix 1 with associated catalog numbers, specimen sizes and localities.

crysos, *C. latus*, and *C. lugubris*) commonly are found at insular localities, including Ascension Island on the mid-Atlantic ridge.

Material examined Two hundred fifty-one specimens (29.5–1070 mm FL) from 103 collections (western Atlantic localities abbreviated). MASSACHUSETTS: ANSP 165909 (4, 152–189); USNM 10431 (4, 262–276); USNM 13656 (265); USNM 126812 (2, 54–69). RHODE ISLAND: ANSP 98280 (2, 175–179); USNM 21654 (274). NEW JERSEY: ANSP 97864 (3, 176–189); ANSP 121305 (2, 167–175); ANSP 105515 (173); ANSP 165911 (118); USNM 37022 (187); USNM 45120 (133); USNM 64053 (186). DELAWARE: USNM 187280 (5, 102–120), Indian River. VIRGINIA: ANSP 52647 (167). NORTH CAROLINA: UF 124148 (153) and UF 124400 (154), Onslow Bay. SOUTH CAROLINA: UF 124149 (122). GEORGIA: UF 126976 (2, 132–133). FLORIDA: CAS 216873 (1015); ANSP 33039 (188); ANSP 93821 (366); ANSP 151093 (6, 186–208); CAS 216873 (1015); USNM 12681 (3, 254–269); USNM 22855 (622); USNM 29986 (372; USNM 53335 (263); USNM 57225 (260); USNM 57294 (2, 176–187); USNM 57295 (2, 172–175); USNM 154847 (167), St. Johns River; USNM 184871 (366); USNM 332457 (2, 390–421), Swannee River, salinity 14 ppt; USNM 362541 (3, 430–490), Caloosahatchee River; USNM 62289 (219); USNM 163601 (227). ALABAMA: ANSP 162288 (9, 810-950); USNM 157710 (4, 138–154). TEXAS: ANSP 99176 (5, 96–105); USNM 708 (10, 30–93); USNM 118497 (122); USNM 144017 (153). BAHAMAS: ANSP 102112 (2, 293–297); ANSP 102762 (657). CUBA: USNM 9867 (177); USNM 19821 (2, 357–386); USNM 132964 (2, 303–400). JAMAICA: USNM 32080 (725). DOMINICAN REPUBLIC: ANSP 81949 (114). PUERTO RICO: ANSP 151589 (254); ANSP 151590 (182). MEXICO: ANSP 159674 (5, 655-717); ANSP 156991 (9, 159–174); USNM 39278 (311); USNM 50473 (281). GUATEMALA: USNM 114580 (333); USNM

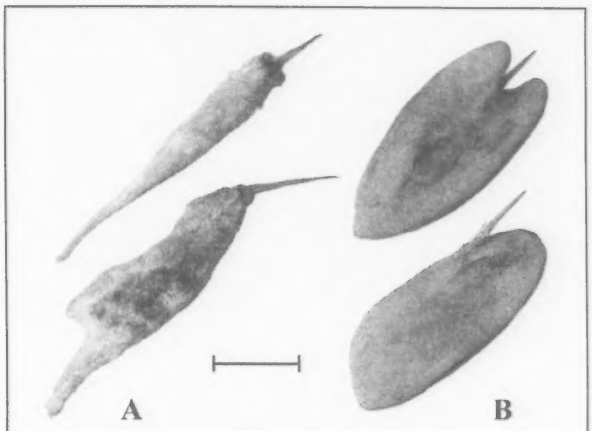


Figure 12

First dorsal-fin pterygiophore of crevalle jack (*Caranx hippos*) in dorsal (above) and lateral (below) views, scale bar = 5 cm: (**A**) USNM 377462, Guinea-Bissau, from 107 cm FL specimen; (**B**) ANSP uncataloged, Atlantic Mexico, from a 36-cm-FL specimen. See discussion of geographic variation in *C. hippos* species account.

114594 (420), 2 mi above mouth of Rio Sarstoon; USNM 114618 (7, 326–557); USNM 134378 (92); USNM 157572 (196). HOUNDURAS: ANSP 158504 (5, 227–251). COSTA RICA: USNM 89073 (122); USNM 94155 (114). PANAMA: ANSP 45238 (2, 119–136); USNM 79965 (287); USNM 79981 (440); USNM 128657 (2, 350–364); USNM 128658 (334). COLOMBIA: USNM 94769 (2, 142–158); USNM 290077 (247). CURACAO: USNM 34914 (263). VENEZUELA: ANSP 161642 (2, 202–209); USNM 121801 (9, 136–213). GUYANA: USNM 186190 (357). FRENCH GUIANA: ANSP 148238 (294). BRAZIL: AMNH 3889 (300), Para Mkt., holotype of *Caranx hippos tropicus*; AMNH 58046 (274); ANSP 121329 (102); CAS 11861 (178); CAS-SU 22133 (4, 223–235); CAS-SU 51828 (2, 216–235); CAS-SU 51830 (231); CAS-SU 53013 (300); CAS-SU 53015 (311); CAS-SU 53016 (3, 316–319); CAS-SU 53025 (233); CAS-SU 53026 (232); CAS-SU 53080 (2, 605–617); CAS-SU 53082 (2, 534–555). MAURITANIA: MNHN 1978-216 (331), Port Etienne. SENEGAL: BMNH 1900.6.28.302–303 (2, 95—109), St. Louise, M. P. Delhez; ZMUC 25 (565), Senegal, Dakar, Dec 1927, H. Madsen. GUINEA-BISSAU: USNM 377462 (estimated 107 cm) anterior dorsal-fin pterygiophore, May 2004, P. Sebile. LIBERIA: ANSP 158494 (16, 29.5–35.0), 6°31′–7°07N′, 11°29′–11°57′30″W, surface dip net, 12 Nov 1963, B. B. Collette, sta. BBC 888. GHANA: CAS-SU 64646 (28, 34.8–68.4), mouth of Volta River at Little Ada, 12 Jan 1963, T. R. Roberts; USNM 373239 (3, 33–52), Volta River at Big Ada, 9 Mar 1960, G. W. Bane; USNM 42228 (71), Ashantee, Beyah River, 27 Nov 1889, W. H. Brown; USNM 373241 (3, 48–57), beach at Tema fishing harbor, 15 Dec 1959, G. W. Bane; USNM 373247 (66), 0.4 km above mouth of Rio Hwini, Takoradi, 26 Nov 1959, G. W. Bane; USNM 300496 (78), Takoradi swimming pool, 10 Aug 1961, G. W. Bane; USNM 368825 (65), Takoradi Fisheries Station bay, 14 Aug 1961, G. W. Bane. NIGERIA: MNHN 1896-328 (150), Campagne Toutee; BMNH 1968.11.15.29-30 (2, 93–94), Lagos Lagoon, 1967, S. O. Fagade. EQUATORIAL GUINEA: MNHN 1893-14 (155), Pobeguin. CONGO: MNHN 1967-0286 (88), Tchitemo, May 1964, A. Stauch. WEST AFRICA: MNHN 1978-230 (274) "coast of tropical French Africa."

Caranx caninus Günther, 1867
Pacific crevalle jack
(Figs. 1C, 6–7, 11, 13–15; Tables 1–4)

Caranx caninus Günther, 1867:601 (original description; Panama; holotype BMNH 1863.12.16.19); Günther, 1868:432 (expanded description); Walford, 1937:72, color pl. 51, Fig. A (diagnosis; comparison with *C. hippos*; habits); Walford, 1974:15 ("disagreement among ichthyologists as to whether species is distinct from *C. hippos*;" distribution); Eschmeyer and Herald, 1983, Fig. 40 (diagnosis; possible synonym of *C. hippos*; distribution); Allen and Robertson, 1994:126, pl. VIII-4 (color photograph; brief description); Franke and Acero, 1993:57 (size at sexual maturity; Colombia); Grove and Lavenberg, 1997:362, Figs. 37 (color), 192, 193 (brief description; Galapagos); Garrison, 2000:166, color photograph (uncommon; Costa Rico, Cocos Island); Lea and Rosenblatt, 2000:122 (occurrence in San Diego Bay).

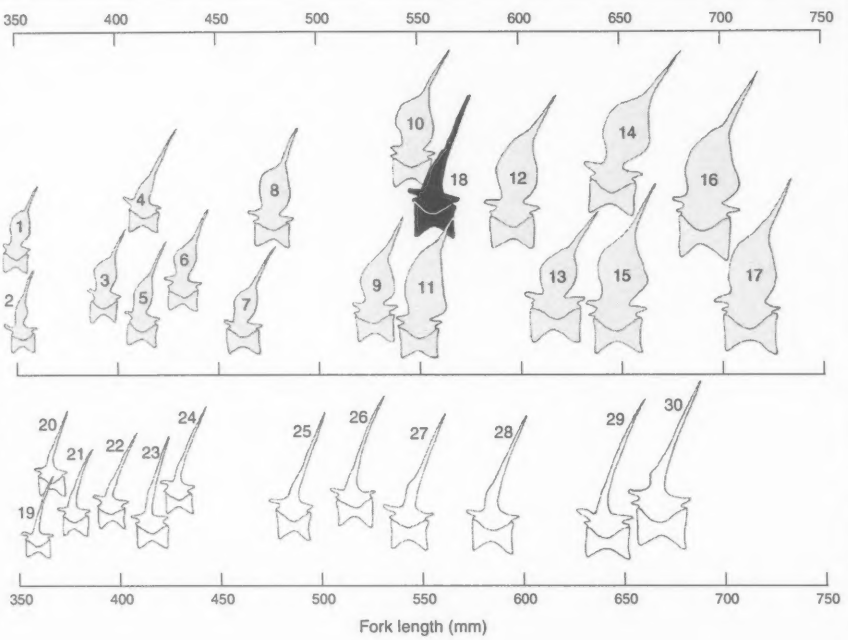


Figure 13

Eighth precaudal vertebra in lateral view (outlines traced from radiographs, anterior to left, plotted against fork length) of crevalle jack (*Caranx hippos*) (vertetra numbers 1–17, western Atlantic; 18, eastern Atlantic, in black; see discussion of geographic variation in species account.) and Pacific crevalle jack (*Caranx caninus*) (19–30). Numbers correspond to those given in Appendix 2 where associated catalog numbers, specimen sizes, and localities are also provided.

Caranx hippos (not of Linnaeus): Jordan and Gilbert, 1883:201 (synonymy; in part; *C. caninus* listed as synonym); Jordan, 1895:432 (misidentification in part; important food fish, occasionally entering estuaries; specimens from west coast and Havana indistinguishable; Mazatlan); Gilbert and Starks, 1904:77 (misidentification in part; Pacific and Atlantic specimens compared and considered conspecific; Panama Bay); Nichols, 1920:44 (Gulf of California fish indistinguishable from those from Atlantic coast); Meek and Hildebrand, 1925:350 (misidentification in part; distribution "Panama, common on both coasts of tropical America"); Hildebrand, 1946:208 (description; Peru); Fierstine, 1968:1, Figs.1–5 (description of dorsal-fin pterygiophore hyperostosis in Miocene deposits and living *Caranx*); Berry, 1974:240 (eastern Pacific and western Atlantic specimens essentially identical); Amezcua-Linares, 1996:88, unnumbered Fig. (description; biology; Mexico); Castro-Aquirre and Balart, 2002:166 (listed; Revillagigedo Islands).

Caranx (*Tricropterus*) *hippos*: Hiyama, 1937:33, color pl. 12 ("often identified to *C. caninus* Günther; reaches 2 feet, abundant, good food fish").

Caranx hippos caninus: Nichols, 1937:58 (specimens from Ecuador compared with Atlantic *C. hippos*); Hobson, 1968:63, fig. 25 (predatory behavior; Gulf of California).

Diagnosis A member of the *Caranx hippos* complex with the following combination of characters: segmented dorsal-fin rays 19–21 (Table 2); segmented anal-fin rays 16 or 17; posttemporal bones, cleithra, and neural spines of vertebrae never hyperossified (Fig. 14); first pterygiophore of dorsal fin distinctly hyperossfied in adults ≥38 cm FL (Figs. 11, 14); first pterygiophore of anal fin distinctly hyperossified, and having a convex anterior profile, in adults >40 cm FL (Figs. 14, B–C, 15); either none or 5th pleural rib only hyperossified (Fig. 14A) in adults ≥38 cm FL; in specimens >20 cm FL, heights of longest dorsal- and anal-fin rays 1.3–1.7 and 1.3–2.0 mm, respectively, in head length; and anal-fin lobe varying from entirely white to brownish-orange in adults.

Comparisons *Caranx caninus* and *C. hippos* have identical or broadly overlapping mensural and meristic values (Tables 2–4), although *C. caninus* usu-

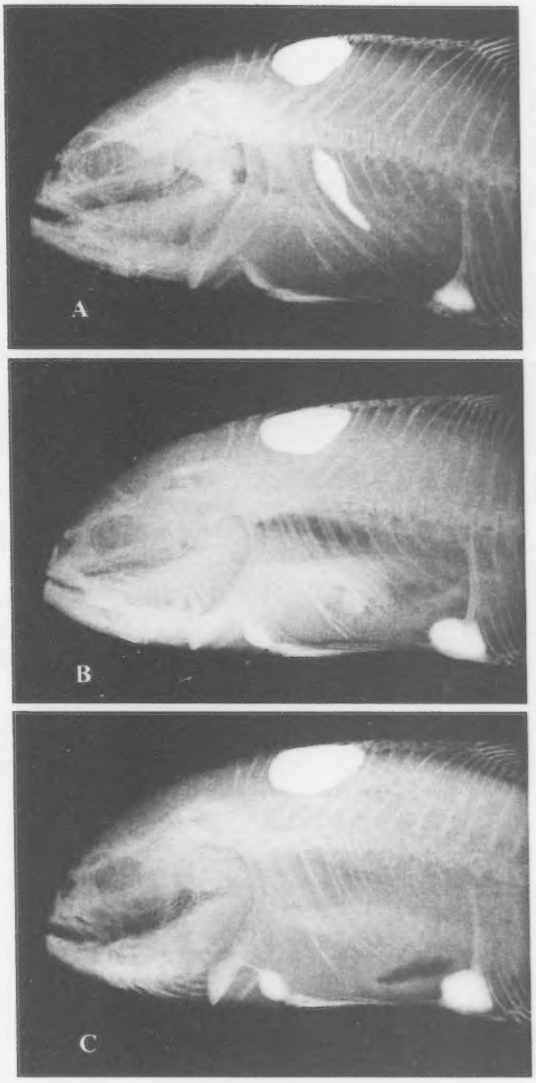


Figure 14

Radiographs of Pacific crevalle jack (*Caranx caninus*) exhibiting hyperostotic bones (pale areas of hyperostotic bones are slightly computer enhanced): (**A**) USNM 100998, 399 mm FL, Mexico; (**B**) USNM 206999, 490 mm FL, Colombia; (**C**) CAS 216871, 538 mm FL, Tres Marias Island.

ally has more lateral-line scutes. Differences in development of hyperostosis (Table 1) are the most useful distinguishing characters (see comparisons in account of *C. hippos*). The color of the anal fin also differs in these two species. In *C. hippos* the anal fin is consistently lemon yellow, fading in postmortem individuals to orange-yellow. The anal fin of *C. caninus* varies from uniformly white to brownish-orange, and often some of the interradial membranes are dark brown. According to photographs of angler-

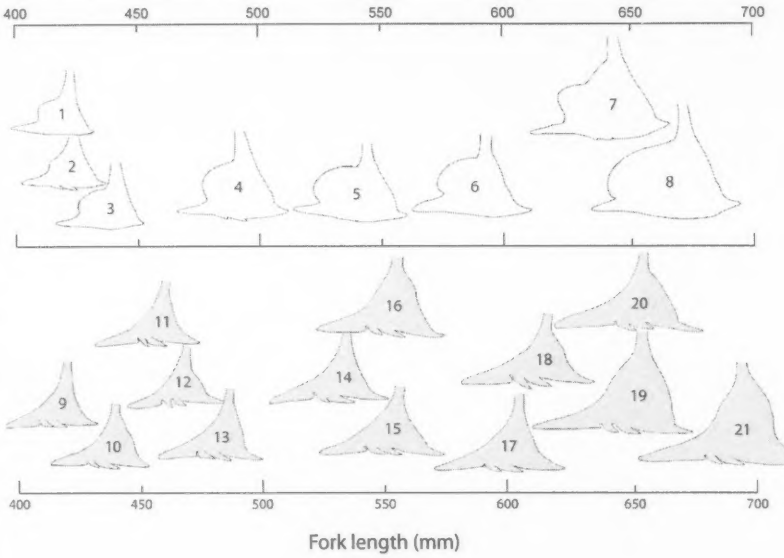


Figure 15

First pterygiophore of anal fin in lateral view (outlines traced from radiographs, anterior to left, plotted against fork length) of Pacific crevalle jack (*Caranx caninus*) (ptergygiophore numbers 1–8) and crevalle jack (*C. hippos*) (9–21). Numbers correspond to those given in Appendix 3 where associated catalog numbers, specimen sizes and localities are also provided.

caught fish, the underside of the caudal peduncle of *C. caninus* is never bright yellow as in *C. hippos,* and in fish with uniformly white anal fins the caudal peduncle is also white.

Remarks We have not had the opportunity to study *C. caninus* in the field although we have examined many color photographs of recently caught adults. The pronounced differences in color of the anal fin in this species (see above) indicate the possibility of sexual dichromatism but determining the sex of large *Caranx* is best done with freshly caught specimens. The striking and inconsistent occurrence of hyperostosis of the third rib in this species (see Table 1) is also puzzling and the possibility that its presence or absence in adults may be sex linked and should be investigated.

Distribution This species is restricted to the eastern tropical Pacific (Fig. 2), ranging north to San Diego Bay, California, where its occurrence is associated with El Niño events (Lea and Rosenblatt, 2000), and from Mexico south to Lobos de Tierra Island, Peru (6°27′S); also known from the Galapagos, Malpelo, Cocos, and Revillagigedo islands, but it is unrecorded from Clipperton Atoll (Robertson and Allen, 1996). Meek and Hildebrand (1925) reported the species, as *C. hippos*, from tidal streams at Corozal and Balboa, Panama.

Material examined One hundred ten specimens (59–670 mm FL) from 51 collections. CALIFORNIA: SIO 75-383 (643), San Diego Bay. TRES MARIAS IS.: CAS 216871 (538); MEXICO: ANSP 144417 (25, 98–176); ANSP 158506 (4, 248-313); CAS 66825 (155); CAS 11112 (329); CAS-SU 55737 (2, 180–182); CAS 216872 (421); SIO 62-61 (3, 372–420); SIO 62-2725 (377); SIO 65-176A (670); SIO 65-182 (431); USNM 28293 (304); USNM 29556 (152); USNM 29617 (156); USNM 47143 (185); USNM 47144 (213); USNM 47145 (191); USNM 100991 (381); USNM 100998 (399); USNM 101006 (261); USNM 205166 (307). GUATEMALA: USNM 114469 (8, 77–233); EL SALVADOR: ANSP 136539 (172); ANSP 144401 (220); ANSP 144406 (169); USNM 220728 (2, 240–248); USNM 367522 (185); USNM 367542 (156); USNM 367671 (81); USNM 367946 (8, 61–77); USNM 367968 (63); USNM 367990 (166). PANAMA: ANSP 144409 (163); CAS 42539 (333); CAS 66826 (177); CAS 89955 (201); USNM 82080 (7, 75–187); USNM 79984 (2, 335–348); USNM 128659 (520); USNM 226417 (4, 59–112); USNM 321987 (2, 67–84). COLOMBIA: ANSP 144413 (164); USNM 206999 (493). ECUADOR: ANSP 158998 (137); CAS 66938 (212). GALAPAGOS IS.: USNM 89751 (2, 109–121), Indefatigable Id. PERU: SIO 58–83 (588); USNM 127917 (158); USNM 127918 (359); USNM 127919 (360).

Table 3

Frequency distributions of lateral-line scales and scutes in the *Caranx hippos* species complex.

	Curved lateral-line scales															
Species	50 51	52 53	54 55	56 57	58 59	60 61	62 63	64 65	66 67	68 69	70 71	72 73	74 75	*n*	$\bar{x}$	SD
C. fischeri	1	—	3	6	6	6	11	8	9	3		1		54	62.1	4.5
C. hippos (E. Atlantic)						1	1	3	1	5	—	1		12	66.2	3.3
C. hippos (W. Atlantic)			1	1	3	7	7	12	14	13	10	4	1	73	66.0	4.1
C. caninus		1	1	—	5	3	9	10	8	4	2	1		44	61.8	4.1

	Straight lateral-line scales															
Species	0 0	1 2	3 4	5 6	7 8	9 10	11 12	13 14	15 16					*n*	$\bar{x}$	SD
C. fischeri	5	6	21	12	19	6	—	—	1					70	5.5	2.8
C. hippos (E. Atlantic)	1	1	4	5	3	2	—	—	1					17	5.9	3.4
C. hippos (W. Atlantic)	4	10	21	19	13	8	5	1	1					82	5.4	3.2
C. caninus	8	9	17	11	7	1	1							54	3.8	2.7

	Straight lateral-line scutes														
Species	24 25	26 27	28 29	30 31	32 33	34 35	36 37	38 39	40 41	42 43	44 45	46 47	*n*	$\bar{x}$	SD
C. fischeri	3	3	15	8	19	17	2	2	1				70	31.8	3.3
C. hippos (E. Atlantic)	4	1	—	6	3	1	2						17	29.9	4.2
C. hippos (W. Atlantic)	1	4	12	26	27	8	3	1					82	31.2	2.4
C. caninus			1	—	—	8	15	16	7	5	1	1	54	38.1	2.9

	Straight lateral-line scales + scutes													
Species	28 29	30 31	32 33	34 35	36 37	38 39	40 41	42 43	44 45	46 47	48 49	*n*	$\bar{x}$	SD
C. fischeri			11	7	24	17	6	3	—	2		70	37.0	3.1
C. hippos (E. Atlantic)	1	1	1	4	4	4	1	1				17	35.8	3.5
C. hippos (W. Atlantic)	1	2	10	18	17	18	12	3	1			82	36.7	3.1
C. caninus	1	—	—	1	4	4	14	13	8	8	1	54	41.9	3.6

Acknowledgments

The study would not have been possible without the generous cooperation of the following individuals who variously facilitated loans and access to specimens, helped with literature, provided accommodations and technical assistance during visits, and general encouragement: M. L. Bauchot, the late F. H. Berry, B. Brown, G. H. Burgess, D. Catania, B. B. Collette, W. E. Eschmeyer, P. C. Heemstra, G. Kelly, T. Iwamoto, R. N. Lea, G. Lenglet, J. G. Lundberg, J. Maclaine, J. G. Nielsen, S. G. Poss, P. Pruvost, R. H. Robins, R. H. Rosenblatt, M. H. Sabaj, J. Schratwieser, O. Schultz, D. G. Smith, V. G. Springer, the late P. J. P. Whitehead, H. Wilkens, and J. T. Williams. Color photographs of *Caranx* spp. were provided by P. Afonso, A. Edwards, G. Kelly (IGFA), J. P. Reid, R. N. Lea, M. Lambouf (FAO), I. Nicholson, E. Truter, and P. Wirtz.

We especially thank H. L. Jelks whose expertise with Photoshop and Adobe Illustrator programs greatly improved the quality of Figures 2, 8, 11–13, and 15, and S. Reardon for digital photography of Figure 12A. We especially thank P. Sebile for his courtesy, with cooperation of the International Game Fish Association, in obtaining and sending us the anterior dorsal-fin spines and pterygiophores of a huge (131 cm TL) *Caranx hippos* from Guinea-Bissau. This material was critical in confirming our preliminary impression that certain aspects of hyperostosis were consistently different in eastern and western Atlantic populations of this species.

Table 4

Frequency distributions for gill raker counts in the *Caranx hippos* species complex.

Species	Upper limb gill rakers: Rudiments 0	1	2	3	4	5	Developed 2	3	4	5	6	7	8	Total 4	5	6	7	8	9	$\bar{x}$
C. fischeri																				
<10 cm FL	18	5	—	1	1			1	1	—	17	6				13	11	1		6.5
>10 cm FL	9	13	7	10	6			3	14	7	4	16	1	1	5	22	17			6.2
C. hippos (E. Atl.)																				
<10 cm FL	8	12	—	3	4				5	2	1	12	7			4	21	2		6.9
>10 cm FL		2	1	2	1			1	2	—	2	1		1	—	2	2	1		6.8
C. hippos (W. Atl.)																				
<10 cm FL	2	1	—	1	1				2	—	—	1	2			1	4			6.8
>10 cm FL	31	28	14	18	9	7	4	11	14	14	26	34	4			10	63	34		7.2
C. caninus																				
<10 cm FL	9	2	1								1	5	6				3	9		7.7
>10 cm FL	9	14	12	10	8	3		4	14	6	9	18	5			1	16	36	3	7.7

Species	Lower limb gill rakers: Rudiments 0	1	2	3	Developed 13	14	15	16	17	18	Total 16	17	18	19	20	$\bar{x}$
C fischeri																
<10 cm FL	4	11	10			3	11	7	4		7	18				16.7
>10 cm FL		2	35	8		14	26	5			10	28	7			17.0
C. hippos (E. Atl.)																
<10 cm FL		13	11	3	1	11	14	1		24	3					16.1
>10 cm FL			5	1	1	4	1			5	1					16.2
C. hippos (W. Atl.)																
<10 cm FL		1	2	2			2	2	1		1	3	1			17.0
>10 cm FL	1	9	80	17		1	35	57	13	1	29	65	13			16.9
C. caninus																
<10 cm FL	4	8							2	6	4		3	9		17.8
>10 cm FL	2	13	38	3			1	10	35	9	1	4	14	31	6	1	17.8

Species	Total gill rakers: Total developed 16	17	18	19	20	21	22	23	24	25	26	Total developed + rudiments 20	21	22	23	24	25	26	27	28	$\bar{x}$
C. fischeri																					
<10 cm FL		1	1	—	—	11	6	4	2					5	10	10					23.2
>10 cm FL	2	6	13	4	5	11	3	1				2	2	9	14	15	3				23.0
C. hippos (E. Atl.)																					
<10 cm FL		3	3	2	6	8		4	1					4	21	2					23.0
>10 cm FL	1	2	1	—	2							1	—	2	2	—	1				22.5
C. hippos (W. Atl.)																					
<10 cm FL	1	1	—	1	—		1	1							2	3					23.6
>10 cm FL	4	6	11	14	12	25	25	9	1					7	15	55	24	6			24.1
C. caninus																					
<10 cm FL							1	1	4	2	4					2	2	8			25.5
>10 cm FL			1	7	12	5	8	12	10	1					2	7	19	21	6	1	25.4

Literature cited

Afonso, P., F. M. Porteiro, R. S. Santos, J. P. Barreiros, J. Worms, and P. Wirtz.
1999. Coastal marine fishes of São Tomé Island (Gulf of Guinea). Bull. Univ. Azores 17A:65–92.

Allen, G. R., and D. R. Robertson.
1994. Fishes of the tropical eastern Pacific, 332 p. Crawford House Press, Bathurst, New South Wales, Australia.

Amezcua-Linares, F.
1996. Peces demersales de la plataforma continental del Pacifico central de México, 184 p. Instituto de ciencias del Mar y Limnología, UNAM/Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D.F.

Arruda, L. M.
1997. Checklist of the marine fishes of the Azores. Arq. Mus. Bocage (n. s.) 3 (2):13–164.

Bauchot, M. L.
1992. Carangidae. *In* Faune des poisons d'eaux douces et saumâtres d'Afrique de l'Ouest, vol. 2 (C. Lévêque, D. Paugy, and G. G. Teugels, eds.), p. 671–875. ORSTOM, Paris.

Bauchot, M. L., and M. Blanc.
1963. Poissons marins de l'Est Atlantique tropical II. Percoidei (Téléostéens Perciformes). 2e partie. Atlantide Rep. 7:37–61.

Bauchot, M. L., and A. Pras.
1980. Guide des poissons marins d'Europe, 427 p. Delachaux et Niestlé, Lausanne-Paris, France.

Bellemans, M., A. Sagna, W. Fischer, and N. Scialabba.
1988. Fiches FAO d'identification des espèces pour les besoins de la pêche. Guide des resources halieutiques du Sénégal et de la Gambie (espèces marines et d'eaux saumâtres), 223 p. FAO, Rome.

Bennett, F. D.
1840. Narrative of a whaling voyage round the globe, from the year 1833 to 1836, vol. 2., 395 p. London.

Berry, F. H.
1959. Young jack crevalles (*Caranx* species) off the southeastern Atlantic coast of the United States. Fish. Bull. 59:417–535.
1960. Scale and scute development of carangid fish *Caranx crysos* (Mitchill). Quart. J. Fla. Acad. Sci. 23:59–66.
1974. Crevalle *Caranx hippos*. *In* McClane's new standard fishing encyclopedia and international angling guide (A. J. McClane, ed.), p. 240–241. Holt, Rinehart, and Winston, New York, NY.

Bianchi, G.
1986. Fichas FAO de identificação de espécies para propósitos comerciais. Guia de campo para as aspécies comerciais marinhas e de águas salobras de Angola, 184 p. FAO, Rome.

Bilecenoglu, M., E. Taskavak, S. Mater, and M. Kaya.
2002. Checklist of the marine fishes of Turkey. Zootaxa 113:1–194.

Bini, G.
1968. Atlante dei pesci delle coste Italiane, vol. 5. Ostetti. Mondo Sommerso, 175 p. Edizioni Calderini, Bologna, Italy.

Blaber, S. J. M.
2002. 'Fish in hot water': the challenges facing fish and fisheries research in tropical estuaries. J. Fish Biol. 61 (suppl. A):1–20.

Blache, J., J. Cadenat, and A. Stauch.
1970. Clés de détermination des poissons de mer signalés dans l'Atlantique oriental entre le 20e parallele nord et le 15e parallele sud. Faune Trop. 18:1–479.

Bloch, M. E.
1793. Naturgeschichte der ausländischen Fische, vol. 7, 144 p. Berlin.

Briggs, J. C.
1960. Fishes of worldwide (circumtropical) distribution. Copeia 1960:171–180.

Brito, A., P. J. Pascual, J. M. Falcón, A. Sancho, and G. Gonzáalez.
2002. Peces de las Islas Canarias catálogo comentado e ilustrado, 419 p. Francisco Lemus, La Laguna, Tenerife, Canary Is.

Cadenat, J.
1950. Poissons de mer du Sénégal. Init. afr. 3:1–345.
1960. Notes d'ichtyologie ouest-africaine. XXX. Poissons de mer ouest-africans observes du Sénégal au Cameroun et plus spécialement au large des Côtes de Sierra Leone et du Ghana. Bull. Inst. fr. Afr. noire, (A) 22 (4):1358–1420.
1961. Notes d'ichtyologie ouest-africaine. XXXIV. Liste complémentaire des espéces de poissons de mer (provenant des côtes de l'Afrique occidentale) en collection a' la section de biologie marine de l'IFAN a' Gorée. Bull. Inst. fr. Afr. noire, (A) 23(1):231–245.

Castro-Aguirre, J. L., and E. F. Balart.
2002. La ictiofauna de las Islas Revillagigedos y sus relacciones zoogeograficas, con comentarios acerca de su origen y evolucioon. *In* Libro Jubilar en Honor al Dr Salvador Contreras Balderas (Lozano-Vilano M de Lourdes, ed.) p. 153–170. Universidad Autonoma de Nuevo Leon, Monterey, Mexico.

Castro-Aguirre, J. L., H. S. Espinosa Pérez, and J. J. Schmitter-Soto.
1999. Ictiofauna estuarino-Lagunar y vicaria de México. Colección Textos Politécnicos. Serie Biotechnologías:1–711.

Cervigón, F.
1993. Los peces marinos de Venezuela, vol. 2., 499 p. Fundación Científica Los Roques, Caracas, Venezuela.

Chabanaud, P., and T. Monod.
1927. Les poissons de Port-Étienne, contribution à la faune ichthyologique de la région du Cap Blanc (Mauritanie Française). Bull. Com. Étud. Hist. Scient. Afr. Occid. Fr. [1926] 9:225–287.

Clark, R. S.
1915. Scottish National Antarctic Expedition: "Scotia" collection of Atlantic fishes. Rep. scient. Results Scott. natn. Antarct. Exped. 4 (16):379–401.

Collignon, J., M. Rossignol, and C. Roux.
1957. Mollusques, crustacès, poisons marins des côtes d'A.E.F. en collection au Centre d'Océanographie de l'Institut d'Etudes Centrafricaines de Pointe-Noire, 396 p. Paris.

Cuvier, G., and A. Valenciennes.
1833. Histoire naturelle des poissons, vol. 9, 519 p. F. G. Levrault, Paris.

Daget, J., and A. Iltis.
1965. Poissons de Côte D'Ivoire (eaux douces et saumâtres). Mém. Inst. Fr. Afr. Noire, (74):385 p.

Daget, J., and A. Stauch.
1968. Poissons d'eaux douces et saumâtres de la region côtière du Congo. Cah. ORSTOM, Hydrobiol. 2 (2):21–50.

Debelius, H.
1997. Mediterranean and Atlantic fish guide, 305 p. IKAN, Frankfurt, Germany.

DeKay, J. E.
1842. Zoology of New-York, or the New-York fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New-York, with brief notices of those occasionally found near its borders, and accompanied by appropriate illustrations. Part IV. Fishes, 415 p. W. & A. White & J. Visscher, Albany, NY.

Desmarest, E.
1856. Reptiles et poissons. *In* Encyclopédie d'histoire naturelle; ou, traité complet de cette science d'après les travaux des naturalistes les plus éeminents de toutes les époques, etc. . . . par le Dr. Chenu. Encyclopédie d'histoire naturelle, vol. 19. (J. G. Chenu, ed.), 360 p. Paris.

Desse, G., F.-J. Meunier, M. Peron, and J. Laroche.
1981. Hyperostose vertebrale chez l'animal. Rhumatologie, 33 (2):105–119.

Devincenzi, G. J.
1924. Peces del Uruguay. II. Nuestra fauna ictiológica segúneuestras colecciones. Anales del Museo N. de Montevideo, ser. 2, 1 (5):139–290.

Duméril, A. H. A.
1861. Reptiles et poissons de la Côte occidentale d'Afrique. Archs. Mus. Hist. Nat. (Paris) 10 [1858]: 241–268.

Edwards, A. J.
1990. Fish and fisheries of Saint Helena Island, 152 p. Centre for Tropical Coastal Management Studies, Univ. Newcastle upon Tyne, Newcastle, England.

Edwards, A. J., A. C. Gill, and P. O. Abohweyere.
2003. A revision of F. R. Irvine's Ghanaian marine fishes in the collections of the Natural History Museum, London. J. Fish Biol. 37:2213–2267.

Edwards, A. J., and C. W. Glass.
1987. The fishes of Saint Helena Island, South Atlantic Ocean. II. The pelagic fishes. J. Nat. Hist. 21:1367–394.

Ehrenbaum, E.
1915. Über küsten Fische von Westafrika, besonders von Kamerun, 85 p, Hamburg, Germany.

Eschmeyer, W. N.
1998. Catalog of fishes, 2905 p. Calif. Acad. Sci., Spec. Publ. 1, San Francisco, California.

Eschmeyer, W. N., and E. S. Herald.
1983. A field guide to Pacific coast fishes of North America, 336 p. Peterson Field Guide Series, No. 28. Houghton Mifflin Co., Boston, MA.

FAO (Food and Agriculture Organization of the United Nations).
2006. Yearbook of fishery statistics—capture production 2004. 98(1):1–560. FAO, Rome.

Fierstine, H. L.
1968. Swollen dorsal fin elements in living and fossil *Caranx* (Teleostei: Carangidae). Cont. Sci. Los Angeles Co. Mus. 137:1–10.

Fischer, W.
1989. The significance of FAO's biosystematics program in the enhancement of world fisheries. Aquatic Sci. 1(4):683–692.

Fowler, H. W.
1919. The fishes of the United States "Eclipse" Expedition to West Africa. Proc. U. S. Natl. Mus. 56 (2294): 195–292.
1936. The marine fishes of West Africa. Bull. Am. Mus. Nat. Hist. 70:1493 p.

Franca, P. da.
1954. Contribuição para o conhecimrento dos Carangídeos (Carangidae, Pomatomidae e Coryphaenidae) de Angola. An. Junta Invest. Ultramar 9 (2):3–52.

Franke, R., and A. Acero P.
1993. Peces Carangoideos del Parque Gorgona, Pacifico Colombiano (Osteichthyes: Carangidae, Nematistiidae y Coryphaenidae). Rev. Biol. Mar., Valparaíso 28:51–73.

Garrison, G.
2000. Peces de la Isla del Cocos [Isla del Cocos fishes], 393 p. INBio, Santo Domingo de Heredia, Costa Rica.

Gilbert, C. H., and E. C. Starks.
1904. The fishes of Panama Bay. Mem. Calif. Acad. Sci. part 4:1–304.

Gill, A. C., and J. M. Kemp.
2002. Widespread Indo-Pacific shore-fish species: a challenger for taxonomists, biogeographers, ecologists, and fishery and conservation managers. Environ. Biol. Fish. 65:165–174.

Gill, T. N.
1862. Note on some genera of fishes of western North America. Proc. Acad. Nat. Sci. Phila. 14:329–332.

Ginsburg, I.
1952. Fishes of the family Carangidae of the northern Gulf of Mexico and three related species. Publ. Inst. Mar. Sci. 2:41–117.

Girard, C. F.
1858. Notes upon various new genera and new species of fishes, in the museum of the Smithsonian Institution, and collected in connection with the United States and Mexican boundary survey: Major William Emory, Commissioner. Proc. Acad. Nat. Sci. Phila. 10:167–171.
1859. Ichthyology. *In* United States and Mexican boundary survey, under the order of Lieut. Col. W. H. Emory, Major First Cavalry and United States commissioner. U.S. and Mexican Boundary Serv. 2 (2):1–85, Fishes pls. 1–41.

Goode, G. B.
1884. The food fishes of the United States. *In* The Fisheries and Fishery Industries of the United States. U.S. Comm. Fish Fish. Rept., Sect. 1 (3):163–682.

Grove, J. S., and R. J. Lavenberg.
1997. The fishes of the Galápagos Islands, 863 p. Stanford Univ. Press, Palo Alto, California.

Gunter, G.
1945. Studies on marine fishes of Texas. Publ. Inst. Mar. Sci. Univ. Texas. 1:1–100.

Günther, A.
1867. On the fishes of the states of Central America, founded upon specimens collected in fresh and marine waters of various parts of that country by Messrs. Salvin and Godman and Capt. J. M. Dow. Proc. Zool. Soc. Lond. 1866 (3):600–604.
1868. An account of the fishes of the states of Central America, based on collections made by Capt. J. M. Dow, F. Godman, Esq., and O. Salvin, Esq. Trans. Zool. Soc. Lond. 6(7):377–494.

Heckel, J. J.
1852. *Caranx carangopis* und fossile Delphin-wirbel. Jahrbuch Geol. Reichsanstalt, Vienna 3 (2):160–161.

Herald, E. S., and R. R. Strickland.
1949. Annotated list of the fishes of Homosassa Springs, Florida. Quart. J. Fla. Acad. Sci. (1948) 11: 99–101.

Hildebrand, S. F.
1939. The Panama Canal as a passageway for fishes,

with lists and remarks on the fishes and invertebrates observed. Zoologica 24 (1):15–45.

1946. A descriptive catalog of the shore fishes of Peru. Bull. U. S. Natl. Mus. 189, 530 p.

Hiyama, Y.

1937. Marine fishes of the Pacific coast of Mexico. (T. Kumada, ed.), 75 p. Nissan Fisheries Institute, Odawara, Japan.

Hobson, E. S.

1968. Predatory behavior of some shore fishes in the Gulf of California. Fish Wildlife Serv. Res. Rep. 73: 1–92.

Hureau, J. C., and E. Tortonese.

1973. Carangidae. *In* Check-list of the fishes of the north-eastern Atlantic and the Mediterranean (CLOFNAM), vol. 1 (Hureau, J. C., and T. Monod, eds.), p. 373–384. UNESCO (United Nations Educational, Scientific, and Cultural Organziation), Paris.

IGFA (International Game Fish Association).

2006. World record game fishes, 2006 ed., 384 p. IGFA, Dania Beach, FL.

Jordan, D. S.

1895. The fishes of Sinaloa. Proc. Calif. Acad. Sci. (ser. 2)5:377–514.

Jordan, D. S., and B. W. Evermann.

1902. American food and game fishes, 573 p. Doubleday, Page & Company, New York, NY.

Jordan, D. S., and C. H. Gilbert.

1883. A review of the American Caranginae. Proc. U. S. Natl. Mus. 6:188–207.

Khan, R. A.

2003. Fish faunal resources of Sunderban estuarine system with special reference to the biology of some commercially important species. Rec. Zool. Surv. India, Misc. Publ., Occas. Pap. 209:1–150.

Klein-MacPhee, G.

2002. Jacks. Family Carangidae. *In* Bigelow and Schroeder's fishes of the Gulf of Maine, 3rd ed. (B. B. Collette, and G. Klein-MacPhee, eds.), p. 411–427. Smithsonian Press, Washington, D.C.

Krishnan, S., and S. S. Mishra.

1994. On a collection of fish from middle and south Andaman group of islands. Rec. Zool. Surv. India 94 (2–4):265–306.

Kwei, E. A.

1978. Food and spawning activity of *Caranx hippos* (L.) off the coast of Ghana. J. Nat. Hist. 12:195–215.

Lacépède, B. G. E.

1801. Histoire naturelle des poissons, vol. 3, 558 p. Plassan, Paris.

Laroche, W.A., J. G. Ditty, J. T. Lamkin, and S. R. Whitcraft.

2006. Carangidae: jacks. *In* Early stages of Atlantic fishes: an identification guide for the western central North Atlantic, vol. 2 (W. J. Richards, ed.), p.1439–1509. CRC Press, Boca Raton, FL.

Lea, R. N., and R. H. Rosenblatt.

2000. Observations on fishes associated with the 1997–98 El Niño off California. Calif. Coop. Oceanic Fish. Invest. Rep. 41:117–129.

Linnaeus, C.

1766. Systema naturae sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Laurentii Salvii, Holmiae. 12th ed., 1(1):1–532.

McBride, R. S., and K. A. Mckown.

2000. Consequences of dispersal of subtropically spawned crevalles jacks, *Caranx hippos*, to temperate estuaries. Fish. Bull. 98:528–538.

Meek, S. E., and S. F. Hildebrand.

1925. The marine fishes of Panama. Part II. Field Mus. Nat. Hist. Publ. Zool. Ser. 15 (226):331–707.

Melliss, J. C.

1875. Class V. Pisces. *In* St. Helena: a physical, historical and topographical description of the island, including its geology, fauna, flora, and meteorology, p. 100–113. Reeve & Co., London.

Menezes, N. A., and J. L. Figueiredo.

1980. Manual de peixes marinhos do sudeste do Brasil. IV. Teleostei (3):1–96.

Mishra, S. S., R. Gouda, L. Nayak, and R. P. Panigrahy.

1999. A check list of the marine and estuarine fishes of south Orissa, east coast of India. Rec. Zool. Surv. India 97 (3):81–90.

Mishra, S. S., and S. Krishnan.

2003. Marine fishes of Pondicherry and Karaikal. Rec. Zool. Surv. India, Occ. Pap. 216:1–52.

Monod, T.

1927. Pisces I, pisces marini. *In* Contributions à l'étude de la faune du Cameroun, part 2 (T. Monod, ed.), p. 643–742. Soc. Edit. Geogr. Marit. Colon., Paris.

Murdy, E. O., R. S. Birdsong, and J. A. Musick.

1997. Fishes of Chesapeake Bay, 324 p. Smithsonian Inst. Press, Washington, D.C.

Nichols, J. T.

1920. On the range and geographic variation of *Caranx hippos*. Copeia (83):44–45.

1937. On *Caranx hippos* (Linnaeus) from Ecuador. Copeia 1937:58–59.

Nichols, J. T., and J. Roemhild.

1946. Fin-count variation in *Caranx hippos* (Linnaeus). Marine Life, Occas. Papers 1(5):15–17.

Norman, J. R., and F. R. Irvine.

1947. Marine fishes. *In* F. R. Irvine, The fishes and fisheries of the Gold Coast, p. 81–220. Crown Agents, London.

Okera, W.

1978. Fishes taken by the beach seines fishing at Lumley, Freetown (Sierra Leone). J. Fish Biol. 12:81–88.

Osório, B.

1911. Peixes colhido nas visinhanças do archipelago de Cabo Verde. Mems Mus. Bocage 3:37–49.

Papaconstantinou, C.

1988. Check-list of marine fishes of Greece, 257 p. Fauna Graeciae IV, Hellenic Zoological Society, Athens.

Peters, W. (C. H.).

1877. Übersicht der während der von 1874 bis 1876 unter dem Commando des Hrn. Capitän z. S. Freiherrn von Schleinitz ausgeführten Reise S. M. S. Gazelle gesammelten und von der Kaiserlichen Admiralität der Königlichen Akademie der Wissenschaften übersandten Fische. Monatsb. Akad. Wiss. Berlin 1876:831–854.

Pellegrin, J.

1907. Mission des pêcheries de la côte occidentale d'Afrique, 2e memoire. Act. Soc. Linn. Bordeaux 62:71–102.

Poll, M.

1954. Poissons. IV. Téléostéens acanthoptérygiens (1ère partie). Résult. Scient. Exped. Océanogr. Belg. Eaux côt. Afr. Atlant. Sud (1948–49) 4(3B):1–390.

Postel, E.
1959. Liste commentée des poissons signalés dans l'Atlantique tropico-oriental nord, du Cap Spartel au Cap Roxo, suivie d'un bref apercu sur leur repartition bathymétique et géographique. Bull. Soc. Scient. Bretagne 34 (1/2):129–170.
Randall, J. E.
1996. Caribbean reef fishes, 3rd ed., 368 p. TFH Publications, Inc., Neptune, NJ.
Robertson, D. R., and G. R. Allen.
1996. Zoogeography of the shorefish fauna of Clipperton Atoll. Coral Reefs (1996) 15:121–131.
Saloman, C. H., and S. P. Naughton.
1984. Food of crevalle jack (*Caranx hippos*) from Florida, Louisiana, and Texas. NOAA Tech. Memo. NMFS-SEFC-134, 34 p.
Sanders, A. L.
1997. Alexander Garden (1730–1791), pioneer naturalist in colonial America. *In* Collection building in ichthyology and herpetology (T. W. Pietsch, and W. D. Anderson Jr., eds.), p. 409–437. Am. Soc. Ich. Herp., Spec. Publ. 3.
Scott, W. B., and M. G. Scott.
1988. Atlantic fishes of Canada. Can. Bull. Fish. Aquat. Sci. 219, 731 p.
Shipp, R. L.
1986. Dr. Bob Shipp's guide to fishes of the Gulf of Mexico, 256 p. 20th Century Printing Co., Mobile, AL.
Smith, C. L.
1985. The inland fishes of New York State, 522 p. New York State Dept. Environ. Conserv., Albany, NY.
Smith-Vaniz, W. F.
1986. Carangidae. *In* Fishes of the north-eastern Atlantic and Mediterranean (FNAM), vol. 2 (Whitehead, P. J. P., M.-L. Bauchot, J.-C. Hureau, J. Nielsen, and E. Tortonese, eds.), p. 815–844. UNESCO (United Nations Educational, Scientific, and Cultural Organization) Paris.
2003. Carangidae. *In* FAO species identification sheets for fishery purposes (K. E. Carpenter, ed.), p. 1426–1468. Western Central Atlantic. FAO, Rome.
Smith-Vaniz, W. F., and F. H. Berry.
1981. Carangidae. *In* FAO species identification sheets for fishery purposes, vol. 1 (W. Fischer and G. Bianchi, eds.), unnumbered p. 1–7+74. Eastern Central Atlantic. FAO, Rome.
Smith-Vaniz, W. F., B. B. Collette, and B. E. Luckhurst.
1999. Fishes of Bermuda: history, zoogeography, annotated checklist, and identification keys. Am. Soc. Ich. Herp., Spec. Publ. 4, 424 p.
Smith-Vaniz, W. F., J. C. Quéro, and M. Desoutter.
1990. Carangidae. *In* Check-list of the fishes of the eastern tropical Atlantic (CLOFETA), vol. 2 (Quéro, J. C., J. C. Hureau, C. Karrer, A. Post, and L. Saldanha, eds.), p. 729–755. UNESCO, Paris.
Smith-Vaniz, W. F., L. S. Kaufman, and J. Glowacki.
1995. Species-specific patterns of hyperostosis in marine teleost fishes. Mar. Biol. 121:573–580.
Steindachner, F.
1859. Beiträge zur Kenntniss der fossilen Fisch-Fauna Österreichs. Sitzungsber. Akad. Wiss Wien 37:673–703.
1870. Zur Fischfauna des Senegal. Erste Abtheilung. Sitzungsber. Akad. Wiss Wien 60 (1) [1869]:669–714.
Talwar, P. K., and R. K. Kacker.
1984. Commercial sea fishes of India, 997 p. Zool. Surv. India, Calcutta.
Thompson, R., and J. L. Munro.
1983. The biology, ecology, and bionomics of the jacks, Carangidae. *In* Caribbean Coral Reef Fishery Resources (J. L. Munro, ed.), p. 82–93. International Center for Living Aquatic Resources Management, Manila, Philippines.
Tortonese, E.
1952. Monografia dei Carangini viventi nel Mediterraneo (Pisces Perciformes). Ann. Mus. Civ. Stor. Nat. Giacomo Doria 65:259–324.
1973. The ichthyological collections now existing in Italy. Ann. Mus. Civ. Stor. Nat. Giacomo Doria 79: 108–116.
1975. Osteichthyes (Pesci ossei). Parte seconda. Edizioni Calderini, Bologna. Fauna Ital. 11:1–636.
Uyeno, T., K. Matsuura, and E. Fujii, eds.
1983. Fishes trawled off Suriname and French Guiana, 519 p. JAMARC (Japan Marine Fishery Resources Research Center), Toyko.
Vergara, R.
1972. Analisis taxonomico y consideraciones filogeneticas sobre las especies Cubanas del genero *Caranx* (teleostel, Perciformes, Carangidae). Cent. Inst. Pesq. Cuba (34):1–137.
Walford, L. A.
1937. Marine game fishes of the Pacific Coast from Alaska to the Equator, 205 p. Univ. Calif. Press, Berkeley, CA.
1974. Marine game fishes of the Pacific Coast from Alaska to the Equator, p. 1–19. [i–xxix+1–205], pls. 1–69. Reprint of 1937 edition for the Smithsonian Institution by T.F.H. Publications, Inc., Neptune, NJ.
Wheeler, A.
1985. The Linnaean fish collection in the Linnaean Society of London. Zool. J. Linn. Soc. 84:1–76.
Williams, F.
1968. Report on the Guinean Trawling Survey. Vol. 1: General report. Lagos:1–828.

Appendix 1

Catalog numbers, localities, and sizes (mm FL) of specimens used for outline drawings of the first dorsal-fin pterygiophore in Figure 11. Numbers in bold correspond to the numbers for the pterygiophores illustrated in Figure 11.

Caranx caninus: **1**, ANSP 144406 (169) El Salvador; **2**, USNM 114469 (178) Guatemala; **3**, USNM 820080 (187) Panama; **4**, USNM 47145 Gulf of California (192); **5**, USNM 114469 Guatemala (197); **6**, CAS 66938 Ecuador (212); **7**, USNM 47144 Gulf of California (213); **8**, ANSP 144401 El Salvador (220); **9**, USNM 114469 Guatemala (227); **10**, USNM 114469 Guatemala (233); **11**, USNM 200728 El Salvador (240); **12**, ANSP 158506 Mexico, Sinalosa (248); **13**, ANSP 158506 Mexico, Sinalosa (258); **14**, USNM 101006 Mexico (261); **15**, ANSP 158506 Mexico, Sinalosa (262); **16**, USNM 28293 Mexico (304); **17**, USNM 205166 Baja California (307); **18**, ANSP 158506 Mexico, Sinalosa (313); **19**, CAS 42539 3º53'N, 105º10'W (333); **20**, CAS 11112 Mexico (329); **21**, US-

NM 79884 Panama (348); **22**, USNM 127918 Peru (359); **23**, USNM 127919 Peru (360); **24**, SIO 62-61 Mexico, Isabel Island (371); **25**, USNM 100991 Mexico (381); **26**, USNM 100998 Mexico (399); **27**, SIO 62-61 Mexico, Isabel Island (419); **28**, CAS 216872 Baja California (421); **29**, SIO 65-182 (431); **30**, SIO-62-61 Mexico, Isabel Island (438); **31**, USNM 206999 Colombia (490); **32**, USNM 128659 Panama (520); **33**, CAS 216871 Tres Marias Island (538); **34**, SIO 58-83 Peru (588); **35**, SIO 75-383 California, San Diego (643); **36**, SIO 65-176A Baja California (670).

Caranx hippos: **37**, USNM 57294 (176) Florida; **38**, ANSP 97864 (176) New Jersey; **39**, ANSP 97864 (189) New Jersey; **40**, ANSP 151093 (198) Florida; **41**, USNM 121801 (205); Venezuela **42**, ANSP 151093 Florida (207); **43**, USNM 121801 (213) Venezuela; **44**, CAS 122133 (223) Brazil; **45**, CAS 122133 (228) Brazil; **46**, ANSP 158504 (233) Honduras; **47**, CAS 122133 (235) Brazil; **48**, ANSP 151589 (254) Puerto Rico; **49**, ANSP 158504 (251) Honduras; **50**, USNM 12681 (254) Key West; **51**, USNM 12681 (269) Key West; **52**, AMNH 3889 (274) Brazil; **53**, ANSP 148238 (294) French Guiana; **54**, ANSP 102112 (298) Brazil; **55**, AMNH 3889 (300) Brazil; **56**, CAS 153016 (316) Brazil; **57**, CAS 153016 (319) Brazil; **58**, USNM 114618 (326) Guatemala; **59**, USNM 114618 (332) Guatemala; **60**, USNM 128658 (334) Panama; **61**, USNM 128658 (350) Panama; **62**, USNM 114618 (360) Guatemala; **63**, USNM 128657 (364) Panama; **64**, ANSP 93821 (366) Florida; **65**, USNM 29986 (372) Rhode Island; **66**, USNM 19821 (386) Cuba; **67**, USNM 132964 (400) Cuba; **68**, USNM 114594 (420) Guatemala; **69**, USNM 332457 (421) Florida; **70**, USNM 362541 (430) Florida; **71**, USNM 79981 Panama (440); **72**, USNM 362541 (460) Florida; **73**, USNM 362541 (470) Florida; **74**, USNM 114816 (485) Guatemala; **75**, CAS 153082 (534) Brazil;**76**, CAS 153082 (555) Brazil; **77**, CAS 153080 (605) Brazil; **78**, CAS 153080 (617) Brazil; **79**, USNM 22855 Gulf of Mexico (622); **80**, ANSP 159674 (655) Mexico; **81**, ANSP 102762 (657) Bahamas; **82**, USNM 32080 (725) Jamaica; **83**, CAS 216873 (1015) Florida; **84**, MNHN 1978-230 (274) "tropical West Africa"; **85**, MNHN 1978-216 (331) Western Sahara; **86**, ZMUC 25 (565) Senegal, Dakar; **87**, USNM 377462 (1070 estimated, 130 cm TL measured), Guinea-Bissau.

Caranx fischeri: **88**, CAS 38375 (159) Nigeria; **89**, USNM 27566 (163) Sierra Leone; **90**, CAS-SU 15885 (171) Cameroon; **91**, ANSP 158493 (173) Gulf of Guinea, Bioko; **92**, ANSP 158493 (182) Bioko; **93**, ANSP 158493 (197) Bioko; **94**, USNM 279566 (203) Sierra Leon; **95**, ANSP 158497 (237) Sierra Leone; **96**, ANSP 158498 (239) Sierra Leone; **97**, BMNH 1939.7.12.12 (271) Gold Coast; **98**, MNHN 1978-260 (313) Senegal; **99**, MNHN 1978-235 (317) "tropical West Africa"; **100**, ANSP 140256 (328) Cameroon; **101**, BMNH 1899.11.27.87 (348) Congo; **102**, BMNH 1927.12.7.49 (358) Ascension Island; **103**, MRAC 87428 (367) Congo; **104**, MRAC 36 (403) Congo; **105**, ZMUC P.46362 (450) Nigeria; **106**, IRSNB 829 (530) Senegal.

Appendix 2

Catalog numbers, localities, and sizes (mm FL) of specimens used for the outline drawings of the eighth precaudal vertebra in Figure. 13. Number in bold correspond to the numbers for the vertebrae illustrated in Figure 13.

Caranx hippos: **1**, USNM 19821 (357), Cuba; **2**, USNM 114618 (360), Guatemala; **3**, USNM (400) Cuba; **4**, USNM 11490 (420) Guatemala; **5**, USNM 3324557 (421) Florida, Swannee River; **6**, USNM 79981 (440), Panama, Colon; **7**, USNM 362541 (470), Florida, Caloosahatchee River; **8**, USNM 115618 (485), Guatemala; **9**, CAS-SU (534) Brazil; **10**, CAS-SU 53082 (555) Brazil; **11**, USNM 114618 (557) Guatemala; **12**, CAS-SU 53080 (605) Brazil; **13**, USNM 22855 (622) Florida, Pensacola; **14**, ANSP 159674 (655) Mexico, Carmen; **15**, ANSP 102762 (657) Bahamas, Andros Island; **16**, ANSP 159674 (698) Mexico, Carmen; **17**, ANSP 159674 (717) Mexico, Carmen; **18**, ZMUC (565) Senegal, Dakar

Caranx caninus: **19**, USNM 127918 (359) Peru, Lobos de Tierra; **20**, SIO-62-61 (371) Mexico, Isabel Island; **21**, USNM 10099 (381), Mexico, Petarabo Bay; **22**, USNM 100998 (399) Mexico; **23**, SIO 62-61 (419) Mexico, Isabel Id.; **24**, SIO 65-182 (431) Mexico, Baja; **25**, USNM 206999 (490) Colombia, Baja Utria; **26**, USNM 128659 (520) Panama, Miraflores Lock; **27**, CAS 216871 (538) Tres Marias Is.; **28**, SIO 58-83 (588) Peru; **29**, SIO 75-383 (643), San Diego Bay; **30**, SIO 65-176A (670), Baja California.

Appendix 3

Catalog numbers, localities, and sizes (mm FL) of specimens used for the outline drawings of the first anal-fin pterygiophore in Figure 15. Numbers in bold font correspond to the numbers for the pterygiophores seen in Figure 15.

Caranx caninus: **1**, SIO-62-61 (419) Mexico, Isabel Island; **2**, CAS 216872 (421) Baja California; **3**, SIO-62-61 (438) Mexico, Isabel Island; **4**, USNM 206999 (490) Colombia; **5**, CAS 21871(538) Tres Marias Island; **6**, SIO 58-83 (588) Peru; **7**, SIO 75-383 (643) California, San Diego; **8**, SIO 65-176A (670) Baja California.

Caranx hippos: **9**, USNM 114594 (420) Guatemala; **10**, USNM 79981 (440) Panama, Colon; **11**, USNM 362541 (460) Florida, Coloosahatchee River; **12**, USNM 362541 (470), Florida, Coloosahatchee River; **13**, USNM 114618 (485) Guatemala; **14**, CAS-SU 53082 (534) Brazil; **15**, CAS-SU 53082 (534) Brazil; **16**, USNM 114618 (557), Guatemala; **17**, CAS-SU 53082 (555) Brazil; **18**, CAS-SU 53080 (617) Brazil; **19**, ANSP 159674 (655) Mexico; **20**, ANSP 102762 (657) Bahamas; **21**, ANSP 159674 (698) Mexico.

Diets of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, 1993–1999

Andrew W. Trites[1]
Donald G. Calkins[2]
Arliss J. Winship[1]

Email address for A. W. Trites: trites@zoology.ubc.ca

[1] Marine Mammal Research Unit, Fisheries Centre
Room 247, AERL – Aquatic Ecosystems Research Laboratory
2202 Main Mall, University of British Columbia
Vancouver, BC, Canada V6T 1Z4

[2] Alaska Department of Fish and Game
333 Raspberry Road
Anchorage, Alaska 99518-1599

Abstract—The diet of Steller sea lions (*Eumetopias jubatus*) was determined from 1494 scats (feces) collected at breeding (rookeries) and nonbreeding (haulout) sites in Southeast Alaska from 1993 to 1999. The most common prey of 61 species identified were walleye pollock (*Theragra chalcogramma*), Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes hexapterus*), Pacific salmon (Salmonidae), arrowtooth flounder (*Atheresthes stomias*), rockfish (*Sebastes* spp.), skates (Rajidae), and cephalopods (squid and octopus). Steller sea lion diets at the three Southeast Alaska rookeries differed significantly from one another. The sea lions consumed the most diverse range of prey categories during summer, and the least diverse during fall. Diet was more diverse in Southeast Alaska during the 1990s than in any other region of Alaska (Gulf of Alaska and Aleutian Islands). Dietary differences between increasing and declining populations of Steller sea lions in Alaska correlate with rates of population change, and add credence to the view that diet may have played a role in the decline of sea lions in the Gulf of Alaska and Aleutian Islands.

Manuscript submitted 10 January 2006 to the Scientific Edfitor's Office.

Manuscript accepted: 6 October 2006 by the Scientific Editor.

Fish. Bull. 105:234–248 (2007).234

Steller sea lion (*Eumetopias jubatus*) populations in the Aleutian Islands and Gulf of Alaska began declining in the mid-1970s and were listed as endangered under the U.S. Endangered Species Act in 1997 (NMFS[1]; Trites and Larkin, 1996; Loughlin, 1998). The cause of the population decline is uncertain but may be linked to a decrease in the quantity, quality, or availability of prey, in turn caused either by commercial fisheries or by a natural change in the ecosystem (Alaska Sea Grant, 1993; DeMaster and Atkinson, 2002; Trites et al., 2007). Stomach contents and scat analysis indicate that the diets of the declining population may have changed from primarily small, fatty, schooling fishes (such as capelin (*Mallotus villosus*) and sand lance (*Ammodytes hexapterus*)) in the 1950s to one increasingly dominated by walleye pollock (*Theragra chalcogramma*), Atka mackerel (*Pleurogrammus monopterygius*), and flatfish (Pleuronectidae) in the 1970s, 1980s, and 1990s (Mathisen et al., 1962; Thorsteinson and Lensink, 1962; Pitcher, 1981; Calkins and Goodwin[1]; Merrick et al., 1997; Sinclair and Zeppelin, 2002).[2]

Merrick et al. (1997) found a positive relationship between the rate of population change and the diversity of summer Steller sea lion diets in the declining population during the early 1990s. Regions that had the highest rates of decline had the lowest diversities of diet. The greater the diet diversity, the slower the rate of population decline. Additional diet data (through to 2001) supported the conclusion that diet diversity had some influence on population success (Sinclair and Zeppelin, 2002; Sinclair et al., 2005). Merrick et al. (1997) hypothesized that animals with less diverse diets may have experienced difficulty obtaining enough prey. Others have hypothesized that consumption of larger proportions of lower energy-dense prey may have exacerbated the effect of diet diversity by increasing the food requirements of sea lions (Alverson, 1992; Rosen and Trites, 2000; Trites and Donnelly, 2003). Sea lions with less diverse, low energy-dense diets may also have been more sensitive to changes in overall prey abundance, and could have theoretically incurred higher rates of predation from killer

[1] NMFS (National Marine Fisheries Service). 1992. Recovery plan for the Steller sea lion (*Eumetopias jubatus*), 92 p. Prepared by the Steller Sea Lion Recovery Team for the National Marine Fisheries Service, 1315 East-West Highway, Silver Spring, MD 20910-3282.

[2] Calkins, D. G., and E. Goodwin. 1988. Investigation of the declining sea lion population in the Gulf of Alaska, 76 p. Unpublished report. Alaska Department of Fish and Game, 333 Raspberry Road, Anchorage, AK 99518-1599.

whales if they had to forage for longer periods of time.

Population trends in Southeast Alaska have been opposite to those observed in the Gulf of Alaska (Trites and Larkin, 1996; Calkins et al., 1999; Pitcher et al., 2007). The robustness of the Southeast population compared to the other regions of Alaska may reflect a difference in diet. One explanation for this finding is that Steller sea lions in Southeast Alaska eat a wider range of prey and therefore have a more diverse diet. Another is that low energy-density prey (such as pollock) do not comprise a significant portion of the sea lion diet in Southeast Alaska.

Our goal was to determine the diets of Steller sea lions in Southeast Alaska. We sought to test two hypotheses: 1) diet in Southeast Alaska is the most diverse of all regions inhabited by Steller sea lions; and 2) pollock is not an important prey species in Southeast Alaska. We also wanted to document prey associations and seasonal changes in diet.

Materials and methods

There are three major breeding areas (rookeries) and over 45 major nonbreeding areas (haulouts) in Southeast Alaska. We collected 1494 scats from 12 haulouts and all three rookeries from 1993 through 1999 (Fig. 1). Some areas, such as the Forrester rookery, were sampled every year, and others were sampled less frequently (Table 1). We grouped our analyses into rookeries and haulouts, and then into subgroups by sample size, location, and frequency of sampling. Haulouts consisted of 12 nonbreeding sites in the inside protected waters of Southeast Alaska (Fig. 1). Rookeries consisted of the three breeding areas in Southeast Alaska (Forrester Island, Hazy Island, and White Sisters Islands).

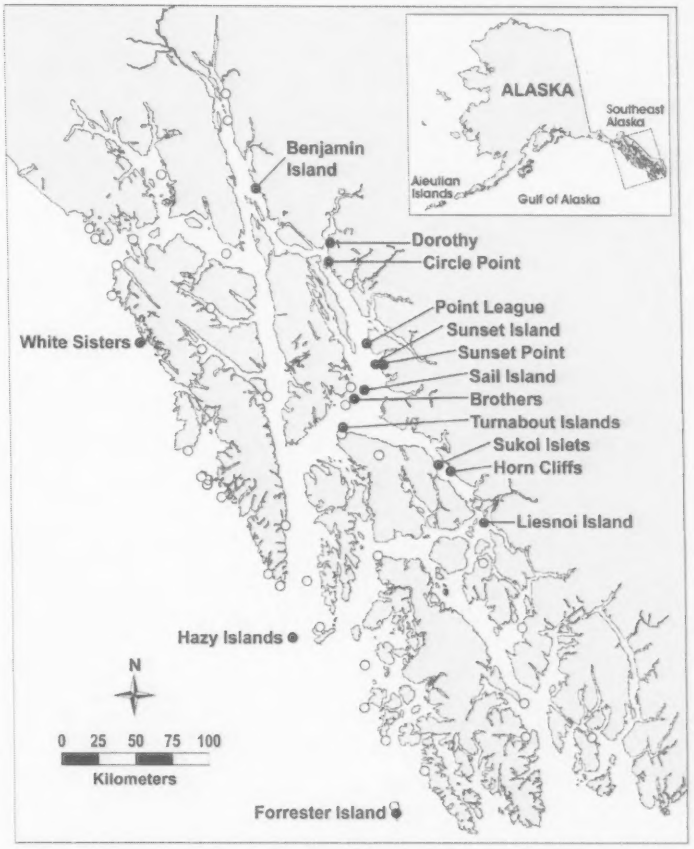


Figure 1

Major rookeries (White Sisters, Hazy Island, and Forrester Island) and haulouts (all other sites) of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska during 1993–99. Labeled sites indicate where scats were collected.

Scats were generally collected opportunistically, when rookeries and haulouts were disturbed in order to count pups or for other research purposes. Each scat was placed in a zip-lock plastic bag and frozen in a 5-gallon plastic bucket before it was shipped to the Food and Energy Consumption Laboratory at the Vancouver Aquarium Marine Science Centre for cleaning. Only scats that were big enough or solid enough to likely contain prey remains were collected, and only one scat was collected from any group of scats if there was any doubt about whether the scat came from more than one Steller sea lion. Each thawed scat was transferred to a plastic jar and soaked in water for 1–6 days. Periodic shaking of the jars ensured that the scats broke down and formed a uniform slurry at the bottom of the jar. Volume was recorded from graduated markings on each jar. An elutriator removed most of the water-soluble elements (Bigg and Olesiuk, 1990) before the remaining sample was washed through a fine mesh screen.

Prey species were identified at Pacific IDentifications Inc. (Victoria, BC) from cleaned and dried hard parts; the types of hard parts that were present and the species from which they came were also noted. Prey hard parts recovered from scats were compared with hard parts from a reference collection of identified skeletal and nonskeletal hard parts. Otoliths and all other hard parts were identified to the lowest possible taxon. Hard parts that were digested beyond recognition or were not diagnostic for prey taxa were not included in our analysis (e.g., ribs). Some recovered structures, such as otoliths or squid beaks, could be used to estimate

the type and number of prey consumed, but other hard parts, such as scales, teeth, branchials, and gill rakers, could only be used to quantify the type of prey consumed.

Scats that were empty or contained prey that could not be identified with certainty were not analyzed. These represented few of the scats collected (56 of 1494, 4%). Unrecognizable hard parts could have been from

Table 1

Total number of Steller sea lion (*Eumetopias jubatus*) scats collected in Southeast Alaska during 1993–99 by year, location, and month. Note that North Rocks, Cape Horn Rocks, and Sea Lion Rocks are part of the Forrester Island rookery complex.

Year	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1993	Benjamin Is.	0	0	0	0	0	0	0	0	0	0	28	0	28
1993	Brothers	0	0	0	0	0	0	0	0	0	7	27	0	34
1993	Cape Horn Rocks	0	0	0	0	0	5	0	0	0	0	0	0	5
1993	Hazy	0	0	0	0	0	27	0	0	0	0	0	0	27
1993	North Rocks	0	0	0	0	0	8	0	0	0	0	0	0	8
1993	Pt. League	0	0	0	0	0	0	0	0	0	0	38	0	38
1993	Sail Is.	0	0	0	0	0	0	0	0	0	0	80	0	80
1993	Sea Lion Rocks	0	0	0	0	0	9	8	0	0	0	0	0	17
	Total	0	0	0	0	0	49	8	0	0	7	173	0	237
1994	Cape Horn Rocks	0	0	0	0	0	29	0	0	0	0	0	0	29
1994	Hazy	0	0	0	0	0	0	54	0	0	0	0	0	54
1994	North Rocks	0	0	0	0	0	32	0	0	0	0	0	0	32
1994	Sea Lion Rocks	0	0	0	0	0	73	0	0	0	0	0	0	73
1994	White Sisters	0	0	0	0	0	0	49	0	0	0	0	0	49
	Total	0	0	0	0	0	134	103	0	0	0	0	0	237
1995	Benjamin Is.	0	0	0	0	0	0	0	0	0	16	0	0	16
1995	Brothers	0	0	0	0	0	0	0	0	0	25	0	14	39
1995	Cape Horn Rocks	0	0	0	0	0	30	0	0	0	0	0	0	30
1995	Circle Pt.	0	0	0	0	0	0	0	0	0	12	0	22	34
1995	Horn Cliff	0	0	0	0	0	0	0	0	0	10	0	0	10
1995	North Rocks	0	0	0	0	0	68	0	0	0	0	0	0	68
1995	Pt. League	0	0	0	0	0	0	0	0	0	13	0	14	27
1995	Sail Is.	0	0	0	0	0	0	0	0	0	26	0	6	32
1995	Sea Lion Rocks	0	0	0	0	0	30	0	0	0	0	0	0	30
1995	Sukoi Is.	0	0	0	0	0	0	0	0	0	7	0	0	7
1995	Sunset Is.	0	0	0	0	0	0	0	0	0	0	0	4	4
1995	Sunset Pt.	0	0	0	0	0	0	0	0	0	0	0	22	22
1995	Turnabout Is.	0	0	0	0	0	0	0	0	0	10	0	2	12
	Total	0	0	0	0	0	128	0	0	0	119	0	84	331
1996	Benjamin Is.	4	0	10	0	0	0	0	0	0	0	0	0	14
1996	Brothers	0	0	15	20	18	0	0	0	0	0	0	0	53
1996	Cape Horn Rocks	0	0	0	0	0	11	13	0	0	0	0	0	24
1996	Dorothy	0	0	0	11	0	0	0	0	0	0	0	0	11
1996	Horn Cliff	0	0	0	0	12	0	0	0	0	0	0	0	12
1996	Liesnoi Is.	0	0	0	0	22	0	0	0	0	0	0	0	22
1996	North Rocks	0	0	0	0	0	0	21	0	0	0	0	0	21
1996	Pt. League	0	0	11	0	14	0	0	0	0	0	0	0	25
1996	Sail Is.	0	0	0	0	11	0	0	0	0	0	0	0	11
1996	Sea Lion Rocks	0	0	0	0	0	8	0	0	0	0	0	0	8
1996	Sunset Pt.	0	0	20	13	0	0	0	0	0	0	45	0	78
1996	Turnabout Is.	0	0	34	0	0	0	0	0	0	0	0	0	34
	Total	4	0	90	44	77	19	34	0	0	0	45	0	313

continued

species not in the reference skeleton collection at the time of identification or could have been too far digested to be identifiable.

We grouped the identified species of prey into eight categories for statistical analysis. These included gadids, forage fish, salmon (Salmonidae), flatfish, rockfish (*Sebastes* spp.), cephalopods, hexagrammids, and other prey (Fig. 2). Scats that contained more than one species from a particular group were scored as containing only a single occurrence of that group. For example, a scat containing both Pacific herring (*Clupea pallasii*) and sand lance was scored as having a single occurrence of forage fish. Hexagrammids do not inhabit the waters of Southeast Alaska in significant numbers but were included as a prey category so that diets could be compared across regions of the North Pacific where hexagrammids are consumed in greater numbers (Merrick et al., 1997; Sinclair and Zeppelin, 2002).

The diversity of the diet was calculated for the eight prey groups by using the Shannon-Wiener species diversity index (Rickleffs and Miller, 2000), which yields a value between 1 and 8, where a value of 1 indicates that only one of the eight groups was consumed, and a value of 8 indicates that all eight were equally consumed. Merrick et al. (1997) used this index to determine the dietary diversity of Steller sea lions that consumed seven prey groups in the Gulf of Alaska and Aleutian Islands. We therefore pooled rockfish with other prey to create the same seven categories used by Merrick et al. (1997) to compare the diversity of diet across all regions of Alaska. We compared our estimate of dietary diversity to those presented by Merrick et al. (1997) for diet data collected between 1990 and 1995. However, we recalculated the diet diversities presented in their paper (from their split-sample frequency of occurrence data) because of a calculation error in their published values.

Seasonal diets were calculated for rookeries in summer (Forrester Island, Jun–Aug, 1993–99) and haulouts in fall (Sep–Nov, 1993 and 1995–96), winter (Dec–Feb, 1996–1997), and spring (Mar–May 1996). Average summer diet (Jun–Aug) was calculated from the three rookeries—weighted by the average number of pups counted at each site during 1993–1997 (pup counts serving as an index of population size; Trites and Larkin, 1996; Pitcher et al., 2007). The summer data were weighted to indicate what the average Steller sea lion ate in Southeast Alaska, rather than to describe what the average rookery diet was. Fall, winter, and spring diets were given equal weight and averaged to describe the nonsummer diet (haulouts, Sep–May) because animals are more evenly distributed during the nonbreeding season and haulout counts were not available for each of the seasons.

The relative importance of prey in the diet was quantified as "simple" and "split-sample" frequency of occurrences. The simple frequency of occurrence indicates what proportion of scats contains any particular prey type. They do not sum to 100%. For example, 80% of the scats examined may contain gadids, and 50% may contain forage fish—meaning that some scats contained both prey types, and others contained only gadids or only forage fish. The second method we used, the split-sample frequency of occurrence (Olesiuk et al., 1990; Olesiuk, 1993), yields the proportion of the overall diet made up of any single prey type. These proportions do sum to 100%. With the split-sample method, it is assumed that the scat contained remains from all prey consumed in the previous meal and that the prey were consumed in equal volumes.

Table 1 (continued)

Year	Location	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1997	Cape Horn Rocks	0	0	0	0	0	25	0	0	0	0	0	0	25
1997	North Rocks	0	0	0	0	0	25	0	0	0	0	0	0	25
1997	Sea Lion Rocks	0	0	0	0	0	25	0	0	0	0	0	0	25
1997	Sunset Pt.	0	32	0	0	0	0	0	0	0	0	0	0	32
1997	Turnabout Is.	0	27	0	0	0	0	0	0	0	0	0	0	27
	Total	0	59	0	0	0	75	0	0	0	0	0	0	134
1998	Cape Horn Rocks	0	0	0	0	0	0	27	0	0	0	0	0	27
1998	Hazy	0	0	0	0	0	0	70	0	0	0	0	0	70
1998	North Rocks	0	0	0	0	0	0	21	0	0	0	0	0	21
1998	Sea Lion Rocks	0	0	0	0	0	0	21	0	0	0	0	0	21
	Total	0	0	0	0	0	0	139	0	0	0	0	0	139
1999	Hazy	0	0	0	0	0	0	60	0	0	0	0	0	60
1999	North Rocks	0	0	0	0	0	6	33	0	0	0	0	0	39
1999	Sea Lion Rocks	0	0	0	0	0	4	0	0	0	0	0	0	4
	Total	0	0	0	0	0	10	93	0	0	0	0	0	103
Grand Total		4	59	90	44	77	415	377	0	0	126	218	84	1494

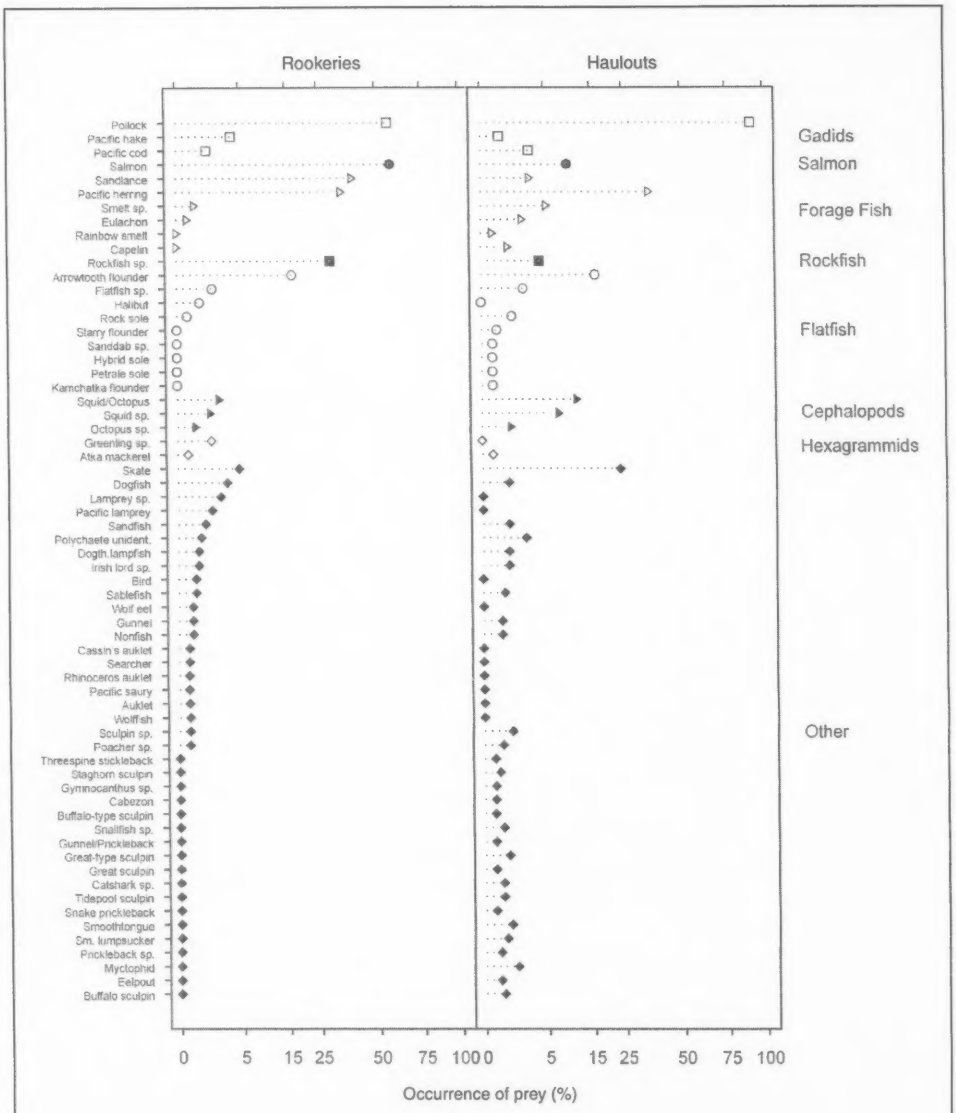


Figure 2

Frequency of occurrence of individual prey species in Steller sea lion (*Eumetopias jubatus*) scats from three Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters; n=752) in summer (Jun–Aug) and haulouts (n=686) during the rest of the year (Sep–May, 1993–99). Data were pooled across months, years, and sites. Plotted data were transformed (square-root transformed) to improve the visual resolution at lower frequencies of occurrence. The eight symbols identify the eight groups of species used to calculate diet diversity.

Statistical analyses were performed on the simple frequency of occurrences to determine whether diets varied by sites and time (across years). We used a contingency table analysis for the total number of scats containing particular prey categories (Pearson χ^2, $\alpha \leq 0.05$). The cephalopod and hexagrammid prey categories were not considered in these analyses because of their low frequencies of occurrence. Differences in the number of categories of prey consumed on each foraging trip (i.e., the number of prey

groups per scat) were compared by using analysis of variance.

Associations between prey groups recovered from individual scats were identified by calculating partial correlation coefficients for each pair of prey groups by using presence and absence data with each scat as a replicate (Zar, 1996). This analysis was performed for all scats collected at the three rookeries during the summer and for all scats collected at the haulouts during autumn–spring. Partial correlations were considered significant at $P=0.05$. Prey associations were illustrated by using the *hclust* function of S-Plus 2000 (Mathsoft Inc., Seattle, WA) and using the "average" clustering method and the distance between two prey groups as equal to 1 minus the partial correlation coefficient of those two prey.

Results

A total of 61 species of prey were identified from all of the scats examined. The most common prey (i.e., those that occurred in more than 5% of all the scats examined) in order of frequency were walleye pollock, Pacific herring, sand lance, salmon, arrowtooth flounder (*Atheresthes stomias*), rockfish (*Sebastes* spp.), skates (Rajidae), squid, and octopus (Fig. 2, Table 2). Species of salmon, rockfish, squids, and octopus could be identified only to family, and other species, such as Pacific herring or walleye pollock, could be identified to species. Unfortunately not all recovered hard parts could be identified to the species level.

Steller sea lion diets at the Forrester Island rookeries were significantly different from one another in 1994 and 1998 ($P<0.001$), but the differences between the diets at Forrester Island and those at Hazy Island in 1993 and 1999 were not significant ($P=0.06$, 0.36, respectively; Fig. 3). At White Sisters, mature females consumed primarily forage fish followed by gadids; whereas at Hazy Island, gadids were the dominant prey. Further south at Forrester Island, the diet was more evenly distributed between forage fish, salmon, and gadids. Scats were collected in multiple years at Forrester Island and Hazy Island and showed little difference in diet over time within each site ($P=0.30$, 0.11, respectively).

Outside of the breeding season, the diet of Steller sea lions in Southeast Alaska was dominated by gadids (primarily pollock; Figs. 4 and 5, Table 3). The abundance of salmon in the diet dropped from summer to fall (Fig. 4, Table 3) when the runs of salmon presumably passed into the river systems. Forage fish were found in 37% of the scats collected in the fall (Sep–Nov), in 43% of scats in the winter, 47% in spring, and in 62% of scats in the summer (Fig. 4). Squid and octopus were more important in fall and winter (22% on average) than during summer. Rockfish were consumed relatively frequently during the summer but were largely absent in the diet from fall to spring, presumably because they were not present or accessible in significant numbers. "Other" fishes (primarily

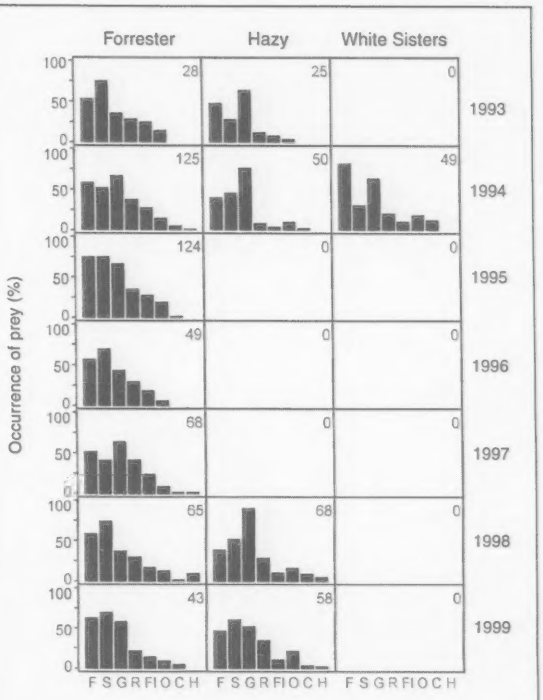


Figure 3

Frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats by year from three Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug). Types of prey consumed were F = forage fish, S = salmon, G = gadids, R = rockfish, Fl = flatfish, O = other, C = cephalopods, and H = hexagrammids. Data were pooled across months. Sample sizes shown in each panel indicate number of scats.

skates, see Fig. 2) rose in importance from summer to fall (13% to 24% respectively), peaking at 50% in winter (Fig. 4). Gadids, forage fishes, and other fishes were the dominant prey during winter. In terms of diet diversity (dd), Steller sea lions consumed the most diverse range of prey categories during summer at rookeries (dd=5.34 on a scale of 1–8), and the least diverse during fall while at haulouts (dd=3.53).

Most scats contained at least two prey groups, and one scat contained remains from all eight groups (Fig. 6). The mean number of prey groups per scat ranged from 2.1 to 2.6 depending on season (Fig. 6). In general, the distributions were skewed towards fewer prey groups occurring together in a single scat in fall and spring, and were more normally distributed in summer and winter. The number of prey types per scat was not significantly different between fall and spring or between summer and winter ($P>0.05$; Tukey-Kramer test) but did differ significantly between these seasonal pairings. Those scats with only a single identifiable prey type

Table 2

Frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats from Southeast Alaska. Samples were from rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug) 1993–99 and from haulouts in fall (Sep–Nov) 1993 and 1995–96, winter (Dec–Feb) 1996–97, and spring (Mar–May) 1996. The rookery data (summer) were pooled across months (and sites within the Forrester complex) but averaged across years and rookeries (weighted by pup counts). Haulout data were pooled across months and sites but averaged across years.

	Frequency of occurrence in diet (%)					Frequency of occurrence in diet (%)			
Species	Summer n=752	Fall n=339	Winter n=143	Spring n=204	Species	Summer n=752	Fall n=339	Winter n=143	Spring n=204
Gadids					Other species				
Walleye pollock	56.4	90.6	96.5	88.7	Skate	4.7	17.7	45.5	18.1
Pacific hake	3.9	0.9	0.0	0.0	Dogfish	3.1	1.5	0.0	0.5
Pacific cod	1.2	2.4	2.1	4.4	Lamprey spp.	2.3	0.0	0.0	0.0
Salmonids					Pacific lamprey	1.5	0.0	0.0	0.0
Salmon	57.7	14.2	4.9	4.4	Sandfish	0.9	0.6	0.0	2.0
Forage fish					Polychaete unident.	0.7	0.6	6.3	2.5
Pacific sand lance	38.8	3.8	2.8	1.5	Dogth lampfish	0.5	0.0	0.7	2.5
Pacific herring	34.0	31.3	39.9	38.2	Irish lord spp.	0.5	0.6	1.4	1.0
Smelt spp.	0.4	5.0	2.8	7.4	Sablefish	0.4	1.2	0.0	0.0
Eulachon	0.1	0.0	2.1	5.4	Wolf eel	0.3	0.0	0.0	0.0
Rainbow smelt	0.0	0.3	0.0	0.0	Gunnel	0.3	0.3	0.7	0.5
Capelin	0.0	0.6	0.0	2.0	Searcher	0.1	0.0	0.0	0.0
Rockfish					Pacific saury	0.1	0.0	0.0	0.0
Rockfish spp.	29.8	1.5	9.1	5.4	Wolffish	0.1	0.0	0.0	0.0
Flatfish					Sculpin spp.	0.1	1.5	1.4	0.0
Arrowtooth flounder	16.8	16.2	20.3	13.2	Poacher spp.	0.1	0.9	0.0	0.0
Flatfish spp.	1.6	1.8	2.1	2.9	Threespine stickleback	0.0	0.0	0.0	0.5
Halibut	0.7	0.0	0.0	0.0	Staghorn sculpin	0.0	0.0	0.0	1.0
Rock sole	0.1	0.9	0.7	2.0	Gymocanthus spp.	0.0	0.0	0.0	0.5
Starry flounder	0.0	0.0	0.0	1.0	Cabezon	0.0	0.0	0.0	0.5
Sanddab spp.	0.0	0.0	0.0	0.5	Buffalo-type sculpin	0.0	0.0	0.0	0.5
Hybrid sole	0.0	0.0	0.0	0.5	Snailfish spp.	0.0	0.0	0.7	1.0
Petrale sole	0.0	0.3	0.0	0.0	Gunnel/Prickleback	0.0	0.0	0.7	0.0
Kamchatka flounder	0.0	0.3	0.0	0.0	Great-type sculpin	0.0	0.0	1.4	1.5
Cephalopods					Great sculpin	0.0	0.0	0.7	0.0
Squid/Octopus	2.1	11.2	20.3	4.4	Catshark spp.	0.0	0.0	1.4	0.5
Squid spp.	1.3	8.0	4.9	7.8	Tidepool sculpin	0.0	0.3	0.7	0.5
Octopus spp.	0.4	1.2	0.0	1.5	Snake prickleback	0.0	0.3	0.0	0.0
Hexagrammids					Smoothtongue	0.0	0.3	2.8	0.5
Greenling spp.	1.5	0.0	0.0	0.0	Small lumpsucker	0.0	0.6	0.7	0.5
Atka mackerel	0.1	0.3	0.0	0.0	Prikleback spp.	0.0	0.3	0.0	0.5
					Myctophid	0.0	1.2	3.5	0.0
					Eelpout	0.0	0.3	0.0	0.5
					Buffalo sculpin	0.0	0.9	0.0	0.0

more likely contained gadids (mostly pollock) than any other species.

There was a positive relationship between scat size (volume) and the numbers of prey types each scat contained for samples <250 mL (which represented about 50% of the scats collected). Beyond this volume, numbers of prey types per scat appeared to be independent of scat size (Fig. 7).

In terms of which prey groups occurred most frequently together, the highest partial correlation among prey groups was between salmon and forage fish (rookeries: r=0.23, $r_{0.05(2),744}$=0.07, P<0.05; haulouts: r=0.189, $r_{0.05(2),678}$= 0.08, P<0.05; Fig. 8). Gadids and cephalopods were also significantly correlated in scats from both rookeries (r=0.11) and haulouts (r=0.08), whereas gadids were negatively correlated with occurrences of salmon

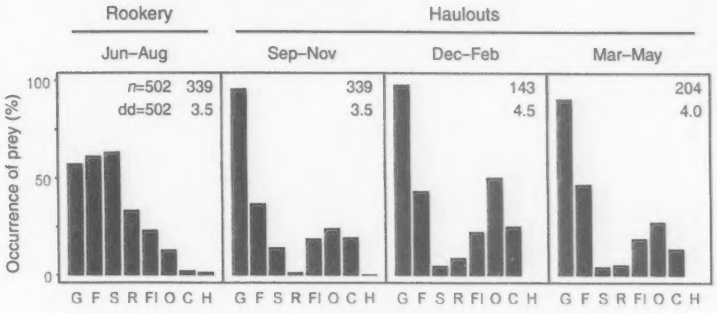


Figure 4

Frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats from the Forrester Island rookery complex (Cape Horn Rocks, North Rocks, and Sea Lion Rocks) in summer (Jun–Aug) 1993–99 and from haulouts in fall (Sep–Nov) 1993, and 1995–96, winter (Dec–Feb) 1996–97, and spring (Mar–May) 1996. Data were pooled for each panel across months, years, and sites. Types of prey consumed were F = forage fish, S = salmon, G = gadids, R = rockfish, Fl = flatfish, O = other, C = cephalopods, and H = hexagrammids. Sample sizes are number of scats, and diet diversity (dd) was calculated using a Shannon-Wiener index and split-sample frequencies of occurrence (Table 3).

Table 3

Split-sample frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats from Southeast Alaska. Samples were from rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug) 1993–99 and from haulouts in fall (Sep–Nov) 1993 and 1995–96, winter (Dec–Feb) 1996–1997, and spring (Mar–May) 1996. The rookery data (summer) were pooled across months (and sites within the Forrester complex) but averaged across years and rookeries (weighted by pup counts). Haulout data were pooled across months and sites, but were averaged across years.

	Prey category (%)							
Season	Cephalopods	Flatfish	Forage fish	Gadids	Hexagrammids	Other	Rockfish	Salmon
Winter (Dec–Feb)	8.1	7.6	13.5	49.1	0.0	15.9	4.5	1.2
Spring (Mar–May)	5.0	7.6	21.0	52.5	0.0	10.5	2.0	1.4
Summer (Jun–Aug)	0.8	6.4	21.9	27.3	0.4	4.3	11.7	27.3
Fall (Sep–Nov)	7.0	6.2	12.5	62.2	0.1	8.4	0.4	3.3

from rookeries (r=−0.16) and with forage fish from scats collected at haulouts (r=−0.10).

Plotting our estimate of dietary diversity for Southeast Alaska during summer with values recalculated for other regions of Alaska revealed a significant relationship between diet diversity and the rate of population change during 1990–94 (Fig. 9). High rates of population decline correlated with low levels of diet diversity.

Discussion

The Southeast Alaska population of Steller sea lions grew considerably since the first census of 100 animals was made at Forrester Island in the 1920s (Rowley, 1929). Subsequent counts were 350 sea lions (nonpups) in 1945 (Imler and Sarber, 1947), and 2500 in 1957 (Mathisen and Lopp, 1963). The total population in 1992 (including pups) was estimated at 10,003 (Trites and Larkin, 1996), and an annual growth rate of 6% was estimated (1979–97; Calkins et al., 1999). Steller sea lions were first noted breeding on White Sisters (3 pups) and Hazy Island (30 pups born) in 1979. In 1997, 205 pups were counted at White Sisters, 1157 were counted at Hazy, and 2798 were counted at Forrester Island. Small numbers of pups have since been noted at Graves Rocks and Biali Rocks (Pitcher et al., 2007).

It is not clear why Steller sea lion populations grew through the 20th century in Southeast Alaska. One possible explanation is that predation by killer whales

or hunting by native peoples was reduced. Another is that these sea lions may have begun consuming more abundant prey or they had a higher quality diet that enhanced birth and survival rates. Unfortunately there is little or no information to shed light on this important question.

There are few data available on fish stocks preyed upon by sea lions or on the diet of Steller sea lions in Southeast Alaska prior to the 1990s. Pollock does not appear to have been abundant in fishery surveys and was not thought to be present in commercially available quantities. However, Imler and Sarber (1947) reported that pollock were found in five of the seven stomachs taken in the vicinity of the Brothers Islands and White Sisters Islands in 1946—and accounted for 68% of the stomach contents by volume. The only other dietary information comes from the stomachs of five Steller sea lions shot at Forrester Island in May 1986 (Calkins and Goodwin[1]); for these sea lions Pacific cod (*Gadus macrocephalus*) accounted for the largest single prey occurrence at 58% of the total volume, and pollock accounted for 32% of the contents by volume and were present in three stomachs.

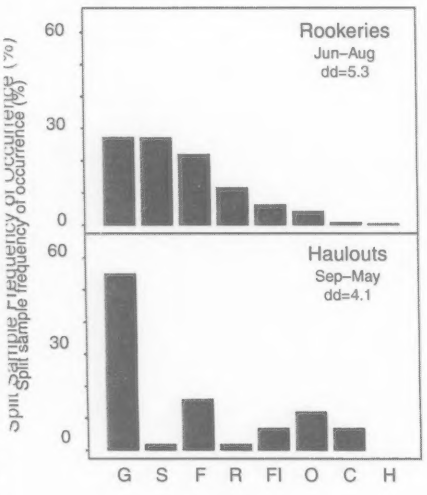


Figure 5

Split-sample frequency of occurrence of prey types in Steller sea lion (*Eumetopias jubatus*) scats from Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug) and from haulouts the rest of the year (Table 1). Diet at rookeries is the weighted average (by the average 1993–97 pup counts) of the three mean rookery diets (averaged across years). The haulout diet is the average of the three mean seasonal diets (averaged across years). Diet diversity (dd) was calculated by using a Shannon-Wiener index. Types of prey consumed were F = forage fish, S = salmon, G = gadids, R = rockfish, Fl = flatfish, O = other, C = cephalopods, and H = hexagrammids.

The scats we collected during the 1990s revealed that gadids were an important part of the diet and that pollock was the predominant gadid. Relatively few Pacific cod were noted (Fig. 2). Pollock were the most frequently occurring food item in all scats examined from haulouts during the nonbreeding season and were second only to salmon by frequency of occurrence in all scats taken from rookeries during the breeding season. Pollock may have been important in the diet of Steller sea lions in the 1940s and 1980s, but the sample sizes taken at that time are inadequate to draw a firm conclusion or to determine whether diet changed over time (Trites and Joy, 2005).

Attempts to reconstruct the size of the pollock consumed during the 1990s in Southeast Alaska from the lengths of bones recovered in the scats revealed that adult fish (>45 cm fork length) were present more frequently in the diets of Steller sea lions on the outer coast sites than they were present in the diets of Steller sea lions from the inside waters (Tollit et al., 2004a). The largest proportions of fish consumed were of adult and subadult sizes. Juvenile pollock (≤20 cm) contributed insignificantly to the overall sea lion diet (Tollit et al., 2004a).

Potential biases

The use of scats, like all measures to quantify diet, entails caveats. Fortunately, the assumptions that underlie our analyses in Southeast Alaska also underlie the interpretation of scats we sought to compare them with from the Gulf of Alaska and Aleutian Islands. Some of the limitations that can restrict the interpretation of the dietary data from scats collected during the 1990s from all parts of Alaska are also greatly reduced by the large sample sizes (>1000 scats) collected in both regions (Trites and Joy, 2005). However, greater caution must be exerted when comparing stomach contents of Steller sea lions shot from the 1950s–1980s with scats collected during the 1990s, particularly for species such as squid and octopus whose beaks can be caught on the stomach lining and are often regurgitated rather than passed through the intestinal tract.

Our seasonal diet estimates largely compared what lactating females were eating during summer with what lactating females and all other age and sex classes were eating during fall, winter, and spring. Whether or not the different age groups forage in different areas or have different prey preferences is not known. It should also be noted that the seasonal descriptions of diet came from samples that were primarily collected in two time periods—February to July (1996–99) and June to December (1993–95). Our conclusions about seasonal changes in diet could therefore be biased if significant changes occurred in the prey field over our decade of sampling. We assumed that feeding conditions remained relatively stable during the 1990s; our conclusions were based on

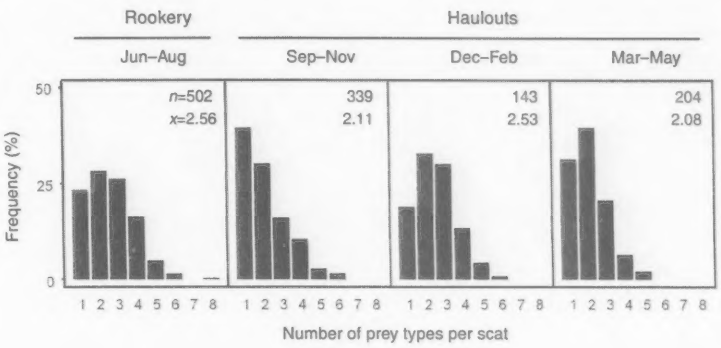


Figure 6

Frequency of number of prey types per Steller sea lion (*Eumetopias jubatus*) scat from the Forrester Island rookery complex in summer (Jun–Aug) 1993–99 and from haulouts in fall (Sep–Nov) 1993 and 1995–96, winter (Dec–Feb) 1996–97, and spring (Mar–May) 1996. Data were pooled for each panel across months, years, and sites. Number of scats collected (n) and mean number of prey per scat ($\bar{x}$) are shown by season.

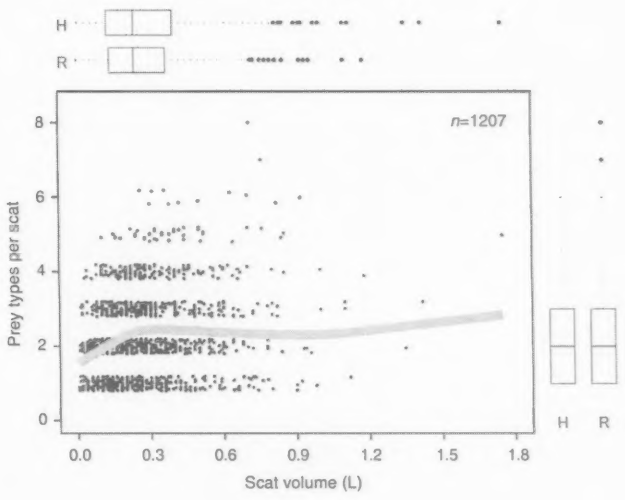


Figure 7

Number of prey types versus volume of Steller sea lion (*Eumetopias jubatus*) scats for three Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters; n=699) in summer (Jun–Aug) and from haulouts (n=508) the rest of the year (Sep–May) during 1994–99 (volume of scat was not measured in 1993). Plotted number of prey types per scat were jittered by adding random variation (0.2) to each value to improve the visual representation of the counts. The fitted line is a locally weighted smoothing of the data (LOWESS, f=2/3). Box plots in the margins show the distribution of scat volume and number of prey types per scat collected at haulouts (H) and rookeries (R).

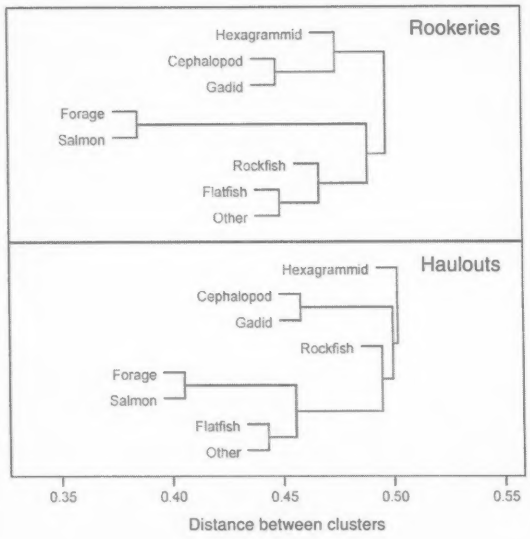


Figure 8

Hierarchal clustering trees of prey groups found in Steller sea lion (*Eumetopias jubatus*) scats from three Southeast Alaskan rookeries (Forrester, Hazy, and White Sisters) in summer (Jun–Aug) and from haulouts the rest of the year (Sep–May). Distances between pairs of prey groups were defined as (1=*partial correlation coefficient*)/2 and clustering was done using "hclust" software (S-Plus 4.0) (MathSoft Inc., Cambridge, MA).

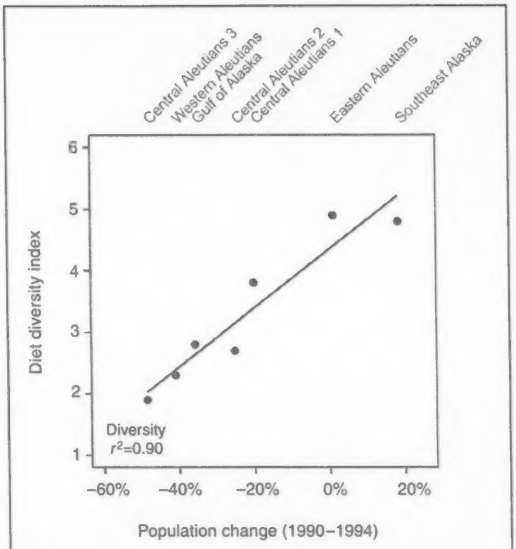


Figure 9

Diet diversity versus rate of population change of Steller sea lions (*Eumetopias jubatus*) between 1990 and 1994 (total number of adults and juveniles counted on rookeries during the summer; Strick et al., 1997) by region of Alaska. The fitted line is a least squares linear regression. Diet diversity was calculated using split-sample frequency of occurrence and a Shannon-Wiener index. The locations and all the data used to calculate diet diversity (except for Southeast Alaska) were taken from Merrick et al. (1997). Data from Southeast Alaska reflect the mean summer rookery diet of Steller sea lions and rockfish were grouped with the "other" prey type.

the consistency of the annual summer diet at Forrester Island (which was sampled in all years, Fig. 2) and on the relative stability of ocean conditions during the 1990s (which is believed to determine the relative abundances of suites of prey available to sea lions and other species; Benson and Trites, 2002; King, 2005; Trites et al., 2007). Thus we feel that the seasonal description of diet accurately reflects what Steller sea lions were eating in Southeast Alaska during the 1990s.

A bias could have been introduced in our analysis if the sizes of collected scats differed significantly between haulouts and rookeries, and if the number of prey species recovered was correlated with the size of scats. In checking this potential source of error, we found numbers of prey types per scat were positively related to size for scats <250 mL but were independent of scat size beyond this volume (Fig. 7). In general, there was little difference in the sizes of scats and numbers of species recovered from rookeries and haulouts, and thus there was no apparent effect of size of scat on our results.

By inferring the dietary importance of prey species from their frequencies of occurrence in scats one implicitly assumes that the probability of finding prey in scats is proportional to the number or mass of that prey consumed, and that this proportionality does not vary among prey species. However, controlled feeding studies with captive Steller sea lions, and other pinnipeds, have shown that the types and proportions of prey hard parts that pass through the digestive tract vary, depending on the species of prey and the size of prey (Cottrell and Trites, 2002; Tollit et al., 2003; Tollit et al., 2004b). Pollock bones, for example, tend to be more robust than the bones of other species and have a higher likelihood of being recovered than the more fragile bones of other species, such as sand lance. However, smaller schooling species, such as sand lance, are likely to be consumed in higher numbers than pollock, and the greater consumption of these smaller species would increase the likelihood of some of the smaller bones passing through the digestive tract. Thus, the probability of detecting different prey species in scats can vary. Recording the presence of all identifiable hard parts as we did (i.e., not relying only on otoliths) significantly reduces the likelihood of any species passing undetected (Cottrell and Trites, 2002).

Captive feeding experiments indicate that the average scat probably contains the remains of prey con-

sumed over a number of days (Tollit et al., 2003). In other words, a scat likely does not represent a single meal, but is probably a composite of one or more feeding trips. Frequency of occurrence (Figs. 2–4) represents the probability that a particular prey type was consumed and does not represent the number or mass of prey consumed. However, with large sample sizes, the ranked importance of any particular prey type appears to equate with frequency of occurrence or numbers of prey (Sinclair et al., 1994; Antonelis et al., 1997; Sinclair and Zeppelin, 2002). The split-sample frequency of occurrence technique is another approach that deals with these biases by assuming that all prey species identified in a scat were consumed in equal mass and that each scat contributes an equal amount of information to the overall diet (Fig. 5, Table 3). Split-sample estimates tend to correlate with simple frequencies of occurrence to give a reasonable proportional description of diet, even when the assumption that all prey in a meal were consumed in equal quantities is not always true.

Prey associations

The remains found in sea lion scats likely delineate associations and distributions of prey species by region. In Southeast Alaska, the hard parts recovered from scats indicate that Steller sea lion prey were not randomly distributed, given that some prey species were found together more frequently than expected (if estimated occurrence was based on chance alone). For example, occurrences of gadids tended to be associated with occurrences of cephalopods (Fig. 8), whereas salmon were found most often with forage fishes (herring and sand lance). An association was also noted between flatfish and "other" species (primarily skates—Figs. 2 and 8). These associations may reflect groups of prey that are commonly associated with each other because of habitat similarities (e.g., depth or substrate similarities).

Associations of prey in scats may also reflect prey-specific foraging strategies of individual Steller sea lions. In some cases, prey associations may reflect secondary prey, whereby a species was consumed by the prey species actually targeted by the sea lion. Hard remains of a fish may occur in a sea lion scat not because it was depredated directly but because it had been consumed by a fish that was then eaten by a sea lion. In our case, 10 of over 60 species were found in more than 5% of the scats and were presumably preferred prey that were directly targeted by the sea lions (Fig. 2). The low frequencies of the remaining 50+ species (Fig. 2) may reflect preferred species that were in low abundance in Southeast Alaska, or they might indicate incidental prey and those that had been consumed by their preferred prey.

Eastern versus western diets

Our systematic survey of Steller sea lion diets in Southeast Alaska during the 1990s was prompted by a desire to gain insight into a possible dietary basis for the population decline that occurred in the Gulf of Alaska and Aleutian Islands. Dietary differences of Steller sea lions between the two regions may help to explain why one population declined while the other increased.

The most common prey of 61 species identified in Southeast Alaska in frequency of occurrence were walleye pollock, Pacific herring, sand lance, salmon, arrowtooth flounder, rockfish, skates, squid, and octopus. Looking further afield (west) we found that Steller sea lions targeted a similar suite of species in the Gulf of Alaska in the 1990s as those we noted in Southeast Alaska, although the relative abundances of each differed considerably (Sinclair and Zeppelin, 2002; Trites et al., 2007). The most common prey reported in the Gulf of Alaska in order of importance were pollock, salmon, Pacific cod, arrowtooth flounder, sand lance, herring, and Irish lords (*Hemilepidotus sp.*). Further west in the Aleutian Islands, however, Atka mackerel, salmon, cephalopods, Pacific cod, Irish lords, and pollock dominated the sea lion diet.

It is unclear what role pollock and Atka mackerel stocks alone have played in the different trajectories of Steller sea lion populations. Pollock were consumed in the Kodiak area—both prior to what was thought to be the beginning of the decline (Pitcher, 1981) and after the decline was under way (Calkins and Goodwin[1]). Calkins and Goodwin[1] noted that although sea lions ate more pollock in the Kodiak area after their decline in terms of frequency of occurrence, the pollock they ate were significantly smaller after the decline began. No similar data are available for Southeast Alaska.

Since the mid 1970s, pollock has been one of the most dominant species in the Bering Sea and Gulf of Alaska ecosystems (Livingston, 1993; Trites et al., 1999; Conners et al., 2002). Unfortunately, little is known about the relative importance of pollock in the Southeast Alaska ecosystem. Pollock have been little exploited, and relatively little is known about their distribution in Southeast Alaska. Surveys conducted during 1950–62 (Alverson et al., 1964) and again during 1976–77 (Parks and Zenger, 1978) caught 64–129 lbs of pollock per hour in select areas of Southeast Alaska using a 400-mesh eastern otter trawl. The 1950–1962 surveys covered only outside waters from Hazy Islands to Dixon Entrance, whereas the later surveys were distributed throughout both inside and outside waters. Parks and Zenger (1978) estimated pollock biomass in Frederick Sound at 0.94 t/nmi[2]. A more recent unpublished estimate indicates that the biomass may have been as much as seven times this level in Frederick Sound in 2001 (Sigler[3]). Thus, pollock would appear to be an important species in the ecosystem within some areas of Southeast Alaska.

The most striking difference between the diets of Steller sea lions in the different regions of Alaska is the diversity of prey consumed. Steller sea lions feed-

[3] M. Sigler. 2004. Personal commun. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Auke Bay Lab, 11305 Glacier Highway, Juneau, AK, 99801.

ing in the Gulf of Alaska and Aleutian Islands during summer had diversity indices of 2–3, compared to 5.3 in Southeast Alaska (Fig. 5, Merrick et al., 1997; Sinclair and Zeppelin, 2002). Summer diets were dominated in the Aleutian Islands by a single species (Atka mackerel) and there were small amounts of other prey in the diet. In the Gulf of Alaska, the dominant prey was pollock, followed by salmon (Sinclair and Zeppelin, 2002). Dietary diversity remained low in the Gulf and Aleutian Islands from summer to winter (Sinclair and Zeppelin, 2002), but dropped in Southeast Alaska from 5.3 to 4.1 (Fig. 5). Winter diets in Southeast Alaska were dominated by pollock. However, the average scat from Southeast Alaska contained at least two prey species. In other words, pollock was rarely consumed alone and, when consumed, was usually accompanied by at least one other species type, such as herring, salmon, sand lance, flatfish, or skates (Figs. 2 and 6).

The inclusion of our data from Southeast Alaska with those from Merrick et al. (1997) provided the same conclusion, namely that the numbers of sea lions declined more slowly and even increased as diversity of diet increased (Fig. 9). Steller sea lions that consumed the least diverse diet experienced the greatest population declines. However, it is not clear whether diet diversity is a proxy for energy content of the sea lion diet as suggested by Winship and Trites (2003), or whether it captures some other biologically meaningful measure of nutrition. Nor is it clear whether the diet diversity index reflects depths of nearest ocean passes to rookeries (with diet diversity increasing with shallower depths; Sinclair et al., 2005), or whether it could be a relative measure of prey distribution and density.

The relative importance of pollock in the diet of Steller sea lions in Southeast Alaska was not expected. However, pollock is not as dominant in the sea lion diet in Southeast Alaska as it is in other regions, and appears to usually be accompanied by other types of energy-rich prey (Fig. 4). It may be easier for sea lions with a more diverse or energy-richer diet to obtain sufficient prey to meet their energy requirements (Trites, 2003; Rosen and Trites, 2004; Trites et al., 2006). They may also be less sensitive to changes in overall prey abundance and may spend less time foraging under risk of predation.

The increase in Steller sea lion numbers in Southeast Alaska since the 1970s contrasts sharply with the declines observed in the Gulf of Alaska. The difference between the diets of Steller sea lions in the two regions is one possible explanation underlying the population trends. Stomach samples collected in the Bering Sea and Gulf of Alaska before the population decline (1950s–mid-1970s) indicate that their diet might have once resembled that of sea lions in Southeast Alaska during the 1990s (Alverson, 1992; Merrick et al., 1997; Sinclair and Zeppelin, 2002). However, the small number of stomachs sampled and the nonstandard methods used to collect them make it difficult to compare pre- and post-decline periods over broad areas. A change in diet during the population decline may be related to large-scale changes in oceanographic conditions (regime shifts) that may have affected the relative abundances of different suites of species (Wilderbuer et al., 2002; King, 2005; Trites et al., 2007). In terms of oceanic regimes, the marine ecosystems of the eastern North Pacific appear to group into two broad domains (California to Southeast Alaska, and the Gulf of Alaska to western Aleutian Islands) that are out of phase with each other as they alternate between anomalous warm and cool states (regimes). Finer-scale analyses should be undertaken to determine how the declines and increases of different prey and predator species line up in time and space with changes in oceanographic events.

Conclusions

A comparison of our dietary data with dietary data collected from other regions of Alaska indicated that Steller sea lions consumed a relatively similar suite of schooling species, most notably pollock, salmon, herring, sand lance, rockfish, and squid. However, in terms of frequency of occurrence, there were marked differences between Southeast Alaska during the 1990s and regions where sea lions have declined. Diets in Southeast Alaska were more diverse and may have had a higher energy content overall. Pollock is part of a normal sea lion diet but is less dominant in Southeast Alaska than in the Gulf of Alaska and Bering Sea where population declines occurred. The difference in diets between the regions is potentially a useful clue for determining why population trends of Steller sea lions have diverged in Alaska. This difference in diets also underlines the overall importance of continuing to assess and monitor sea lion diets.

Acknowledgments

We are grateful to the many people who helped collect and clean the scat, and would particularly like to acknowledge and thank W. Cunningham, D. McAllister, B. Porter, D. Porter, and S. Stanford. We thank P. Rosenbaum for managing our scat collection, and S. Crockford (Pacific IDentifications) for identifying the prey and patiently answering our questions. We are also grateful to M. Rehberg and S. Heaslip for assisting with the map, and M. Sigler for his insights into pollock distribution in Southeast Alaska. Useful comments and suggestions on earlier drafts of our manuscript were made by D. Tollit, D. Rosen, and three anonymous reviewers. Laboratory space was provided by the Vancouver Aquarium Marine Science Centre, and funding was provided by the National Oceanic and Atmospheric Administration to the North Pacific Marine Science Foundation and to the Alaska Department of Fish and Game. Additional support was also provided by the North Pacific Marine Science Foundation through the North Pacific Universities Marine Mammal Research Consortium. Research was conducted under U.S. Marine Mammal Act and Endan-

gered Species Act permits 965 and 358-1564 issued to the Alaska Department of Fish and Game.

Literature cited

Alaska Sea Grant.
1993. Is it food? Addressing marine mammal and sea bird declines, 65 p. Alaska Sea Grant Rep. 93-01. Univ. Alaska Fairbanks, Fairbanks, AK.

Alverson, D. L.
1992. A review of commercial fisheries and the Steller sea lion (*Eumetopias jubatus*): the conflict arena. Rev. Aquat. Sci. 6:203–256.

Alverson, D. L., A. T. Pruter, and L. L. Ronholt.
1964. A study of demersal fishes and fisheries of the northeast Pacific Ocean, 190 p. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, BC.

Antonelis, G. A., E. H. Sinclair, R. R. Ream, and B. W. Robson.
1997. Inter-island variability in the diet of female northern fur seals (*Callorhinus ursinus*) in the Bering Sea. J. Zool., Lond. 242:435–451.

Benson, A. J., and A. W. Trites.
2002. Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean. Fish Fisher. 3:95–113.

Bigg, M. A., and P. F. Olesiuk.
1990. An enclosed elutriator for processing marine mammal scats. Mar. Mamm. Sci. 6:350–355.

Calkins, D. G., D. C. McAllister, K. W. Pitcher, and G. W. Pendleton.
1999. Steller sea lion status and trend in Southeast Alaska: 1979–1997. Mar. Mamm. Sci. 15:462–477.

Conners, M. E., A. B. Hollowed, and E. Brown.
2002. Retrospective analysis of Bering Sea bottom trawl surveys: regime shift and ecosystem reorganization. Prog. Oceanogr. 55:209–222.

Cottrell, P. E., and A. W. Trites.
2002. Classifying prey hard part structures recovered from fecal remains of captive Steller sea lions (*Eumetopias jubatus*). Mar. Mamm. Sci. 18:525–539.

DeMaster, D., and S. Atkinson, eds.
2002. Steller sea lion decline: is it food II?, 80 p. Univ. Alaska Sea Grant, AK-SG-02-02, Fairbanks, AK.

Imler, R. H., and H. R. Sarber.
1947. Harbor seals and sea lions in Alaska, 23 p. U.S. Fish and Wildlife Service, Special Report no. 28.

King, J. R., ed.
2005. Report of the study group on "Fisheries and ecosystem response to recent regime shifts," 168 p. PICES Scientific Report no. 28, Victoria, BC.

Livingston, P. A.
1993. Importance of predation by groundfish, marine mammals and birds on walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea pallasi* in the eastern Bering Sea. Mar. Ecol. Prog. Ser. 102:205–215.

Loughlin, T. R.
1998. The Steller sea lion: a declining species. Bios. Cons. 1:91–98.

Mathisen, O. A., R. T. Baade, and R. J. Lopp.
1962. Breeding habits, growth and stomach contents of the Steller sea lion in Alaska. J. Mammal. 43:469–477.

Mathisen, O. A., and R. J. Lopp.
1963. Photographic census of the Steller sea lion herds in Alaska, 1956–58, 20 p. U.S. Fish and Wildlife Service, Special Scientific Report F-424.

Merrick, R. L., M. K. Chumbley, and G. V. Byrd.
1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: a potential relationship. Can. J. Fish. Aquat. Sci. 54:1342–1348.

Olesiuk, P. F.
1993. Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. Fish. Bull. 91:491–515.

Olesiuk, P. F., M. A. Bigg, G. M. Ellis, S. J. Crockford, and R. J. Wigen.
1990. An assessment of the feeding habits of harbour seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia, based on scat analysis, 135 p. Can. Tech. Rep. Fish. Aquat. Sci. no. 1730.

Parks, N. B., and H. H. Zenger.
1978. Trawl surveys of groundfish resources in the eastern Gulf of Alaska and southeastern Alaskan waters 1976–77, 53 p. Northwest and Alaska Fisheries Science Center Processed Report.

Pitcher, K. W.
1981. Prey of the Steller sea lion, *Eumetopias jubatus*, in the Gulf of Alaska. Fish. Bull. 79:467–472.

Pitcher, K. W., P. F. Olesiuk, R. F. Brown, M. S. Lowry, S. J. Jeffries, J. L. Sease, W. L. Perryman, C. E. Stinchcomb, and L. F. Lowry.
2007. Abundance and distribution of the eastern North Pacific Steller sea lion (*Eumetopias jubatus*) population. Fish. Bull. 105:102–115.

Rickleffs, R. E., and G. L. Miller.
2000. Ecology, 4th ed., 822 p. W. H. Freeman and Company, New York, NY.

Rosen, D. A. S., and A. W. Trites.
2000. Pollock and the decline of Steller sea lions: testing the junk-food hypothesis. Can. J. Zool. 78:1243–1258.

Rosen, D. A. S., and A. W. Trites.
2004. Satiation and compensation for short-term changes in food quality and availability in young Steller sea lions (*Eumetopias jubatus*). Can. J. Zool. 82:1061–1069.

Rowley, J.
1929. Life history of sea lions on the California coast. J. Mammal. 10:1–36.

Sinclair, E. H., T. R. Loughlin, and W. Pearcy.
1994. Prey selection by northern fur seals (*Callorhinus ursinus*) in the eastern Bering Sea. Fish. Bull. 92: 132–156.

Sinclair, E. H., S. E. Moore, N. A. Friday, T. K. Zeppelin, and J. M. Waite.
2005. Do patterns of Steller sea lion (*Eumetopias jubatus*) diet, population trend and cetacean occurrence reflect oceanographic domains from the Alaska Peninsula to the central Aleutian Islands? Fish. Oceanog. 14:223–242.

Sinclair, E. H., and T. K. Zeppelin.
2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). J. Mammal. 83:973–990.

Strick, J. M., L. W. Fritz, and J. P. Lewis.
1997. Aerial and ship-based surveys of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska, the Gulf of Alaska and Aleutian Islands during June and July 1994. NOAA Tech. Memo. NMFS-AFSC-71, 55 p.

Thorsteinson, F. V., and C. J. Lensink.
1962. Biological observations of Steller sea lions taken during an experimental harvest. J. Wildl. Manage. 26:353–359.

Tollit, D. J., S. G. Heaslip, and A. W. Trites.
2004a. Sizes of walleye pollock (*Theragra chalcogramma*) consumed by the eastern stock of Steller sea lions (*Eumetopias jubatus*) in Southeast Alaska from 1994–1999. Fish. Bull. 102:522–532.

Tollit, D. J., S. Heaslip, T. Zepplelin, R. Joy, K. Call, and A. W. Trites.
2004b. A method to improve size estimates of walleye pollock (*Theragra chalcogramma*) and Atka mackerel (*Pleurogrammus monopterygius*) consumed by pinnipeds: digestion correction factors applied to bones and otoliths recovered in scats. Fish. Bull. 102:498–508.

Tollit, D. J., M. Wong, A. J. Winship, D. A. S. Rosen, and A. W. Trites.
2003. Quantifying errors associated with using prey skeletal structures from fecal samples to determine the diet of Steller's sea lion (*Eumetopias jubatus*). Mar. Mamm. Sci. 19:724–744.

Trites, A. W.
2003. Food webs in the ocean: who eats whom and how much? *In* Responsible Fisheries in the Marine Ecosystem (M. Sinclair, and G. Valdimarsson, eds.), p. 125–143. FAO, Rome, and CABI Publishing, Wallingford, UK.

Trites, A. W., and C. P. Donnelly.
2003. The decline of Steller sea lions *Eumetopias jubatus* in Alaska: a review of the nutritional stress hypothesis. Mamm. Rev. 33:3–28.

Trites, A. W., and R. Joy.
2005. Dietary analysis from fecal samples: how many scats are enough? J. Mammal. 86:704–712.

Trites, A. W., and P. A. Larkin.
1996. Changes in the abundance of Steller sea lions (*Eumetopias jubatus*) in Alaska from 1956 to 1992: How many were there? Aquat. Mamm. 22:153–166.

Trites, A. W., P. A. Livingston, S. Mackinson, M. C. Vasconcellos, A. M. Springer, and D. Pauly.
1999. Ecosystem change and the decline of marine mammals in the eastern Bering Sea: testing the ecosystem shift and commercial whaling hypotheses, 106 p. Fisheries Centre Research Reports no. 7(1).

Trites, A. W., A. J. Miller, H. D. G. Maschner, M. A. Alexander, S. J. Bograd, J. A. Calder, A. Capotondi, K. O. Coyle, E. D. Lorenzo, B. P. Finney, E. J. Gregr, C. E. Grosch, S. R. Hare, G. L. Hunt, J. Jahncke, N. B. Kachel, H.-J. Kim, C. Ladd, N. J. Mantua, C. Marzban, W. Maslowski, R. Mendelssohn, D. J. Neilson, S. R. Okkonen, J. E. Overland, K. L. Reedy-Maschner, T. C. Royer, F. B. Schwing, J. X. L. Wang, and A. J. Winship.
2007. Bottom-up forcing and the decline of Steller sea lions (*Eumetopias jubatus*) in Alaska: assessing the ocean climate hypothesis. Fish. Oceanog. 16:46–67.

Trites, A. W., B. P. Porter, V. B. Deecke, A. P. Coombs, M. L. Marcotte, and D. A. S. Rosen.
2006. Insights into the timing of weaning and the attendance patterns of lactating Steller sea lions (*Eumetopias jubatus*) in Alaska during winter, spring, and summer. Aquat. Mamm. 32:85–97.

Wilderbuer, T. K., A. B. Hollowed, W. J. Ingraham, P. D. Spencer, M. E. Conners, N. A. Bond, and G. E. Walters.
2002. Flatfish recruitment response to decadal climatic variability and ocean conditions in the eastern Bering Sea. Prog. Oceanogr. 55:235–247.

Winship, A. J., and A. W. Trites.
2003. Prey consumption of Steller sea lions (*Eumetopias jubatus*) off Alaska: How much prey do they require? Fish. Bull. 101:147–167.

Zar, J. H.
1996. Biostatistical analysis, 3rd ed., 662 p. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Spawning and early development of captive yellowfin tuna (*Thunnus albacares*)

Daniel Margulies (contact author)[1]
Jenny M. Suter[1]
Sharon L. Hunt[1]
Robert J. Olson[1]
Vernon P. Scholey[2]
Jeanne B. Wexler[1]
Akio Nakazawa[3]

Email address for D. Margulies: dmargulies@iattc.org

[1] Inter-American Tropical Tuna Commission
8604 La Jolla Shores Drive
La Jolla, California 92037-1508

[2] Inter-American Tropical Tuna Commission
Achotines Laboratory, Las Tablas
Los Santos Province, Republic of Panama

[3] Overseas Fishery Cooperation Foundation
Sankaido Building, 9-13 Akasaka 1, Minato-ku
Tokyo 107-0052, Japan

Abstract—In this study we describe the courtship and spawning behaviors of captive yellowfin tuna (*Thunnus albacares*), their spawning periodicity, the influence of physical and biological factors on spawning and hatching, and egg and early-larval development of this species at the Achotines Laboratory, Republic of Panama, during October 1996 through March 2000. Spawning occurred almost daily over extended periods and at water temperatures from 23.3° to 29.7°C. Water temperature appeared to be the main exogenous factor controlling the occurrence and timing of spawning. Courtship and spawning behaviors were ritualized and consistent among three groups of broodstock over 3.5 years. For any date, the time of day of spawning (range: 1330 to 2130 h) was predictable from mean daily water temperature, and 95% of hatching occurred the next day between 1500 and 1900 h. We estimated that females at first spawning averaged 1.6–2.0 years of age. Over short time periods (<1 month), spawning females increased their egg production from 30% to 234% in response to short-term increases in daily food ration of 9% to 33%. Egg diameter, notochord length (NL) at hatching, NL at first feeding, and dry weights of these stages were estimated. Water temperature was significantly, inversely related to egg size, egg-stage duration, larval size at hatching, and yolksac larval duration.

Manuscript submitted 15 July 2005 to the Scientific Editor's Office.

Manuscript approved for publication 10 October 2006 by the Scientific Editor.

Fish. Bull. 105:249–265 (2007).

The yellowfin tuna (*Thunnus albacares*) is found worldwide in tropical and subtropical oceans. Yellowfin tuna reproduction is characterized by serial batch spawning and asynchronous oocyte development that is typical of tunas (Schaefer, 2001a). Yellowfin tuna are broadcast spawners and exhibit extremely high batch and annual fecundities over protracted spawning seasons (McPherson, 1991; Schaefer 1996, 1998).

Tuna reproduction has been studied predominantly through histological analyses of the gonads of fish sampled at sea. Estimates have been made of either spawning seasons, spawning intervals, fecundities, or energetic costs of spawning for yellowfin tuna (Joseph, 1963; McPherson, 1991; Schaefer, 1996), skipjack tuna, *Katsuwonus pelamis* (Goldberg and Au, 1986; Hunter et al., 1986; Schaefer, 2001b), bigeye tuna, *Thunnus obesus* (Nikaido et al., 1991), albacore, *Thunnus alalunga* (Ramon and Bailey, 1996), and southern bluefin tuna, *Thunnus maccoyii* (Farley and Davis, 1998). Egg and early larval development of tunas has been described in a number of identification guides or descriptive reviews (Nishikawa and Rimmer, 1987; Ambrose, 1996; Richards, 2006). Most descriptions of early life stages of tunas are based on examinations of specimens collected at sea.

Our knowledge of the spawning dynamics and early development of tunas remains incomplete, and most of our understanding comes from studies of cultured tunas. Before 1980, there were several small-scale efforts in Japan to artificially spawn tunas and to rear the larvae and juveniles (Harada[1]). In the past decade several programs have been developed worldwide to induce spawning and to rear tunas in captivity. Maturation and spawning of tuna broodstock in sea pens in Japan has been described

[1] Harada, T. 1980. Progress and future prospects in tuna culturing studies. *In* Proceedings of the 1979 Japan Tuna Research Conference, Shimizu, Japan, p. 50–58. [Engl. Transl. no. 50 by T. Otsu, 1980, 8 p., avail. Pacific Islands Fisheries Science Center, National Marine Fisheries Service, 2570 Dole Street, Honolulu, HI 96822.]

for yellowfin (Masuma et al.[2]) and bluefin tuna, *Thunnus thynnus* (Miyashita et al., 2000a). Spawning of captive yellowfin tuna in landbased tanks in Bali occurred in late 2004 (Nakazawa[3]). Descriptions of larval and juvenile development stemming from these culturing programs have been presented for yellowfin tuna (Kaji et al., 1999; Margulies et al., 2001; Wexler et al., 2001) and bluefin (Kaji et al., 1996; Miyashita et al., 2001).

Little is known about the spawning behavior of tunas or the influence of physical factors on spawning or egg and larval development. Almost nothing is known about the manner in which tunas aggregate for spawning, their courtship and spawning behaviors, the duration of spawning events, or the effects of physical variables on spawning dynamics or early life stage development. Since 1996, the Inter-American Tropical Tuna Commission (IATTC) has maintained a spawning population of yellowfin tuna in large landbased tanks at the Achotines Laboratory in Panama (Scholey et al., 2001; Wexler et al., 2003). Our broodstock yellowfin tuna have spawned over protracted time periods (nearly year-round on a daily basis) since October of 1996. This spawning pattern has provided a unique opportunity to study the daily spawning dynamics of this species over multiple years. In this article we describe the courtship and spawning behaviors of captive yellowfin tuna, their spawning periodicity, the influence of physical and biological factors on spawning and hatching, and the egg and early-larval development of this species.

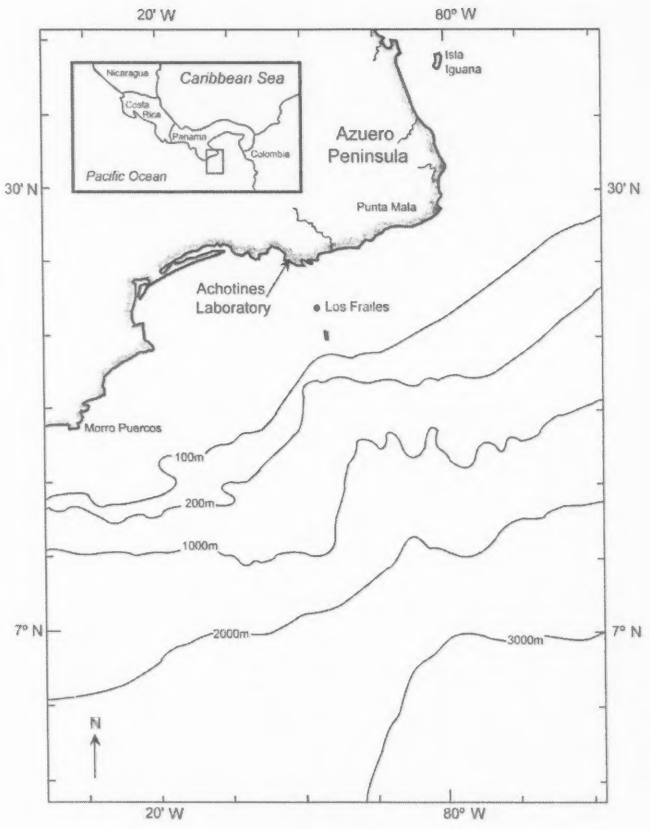


Figure 1

Location of the Inter-American Tropical Tuna Commission's Achotines Laboratory, Republic of Panama.

Materials and methods

Development of the broodstock

The yellowfin tuna broodstock was developed at the IATTC's Achotines Laboratory, located at the southern tip of the Azuero Peninsula of Panama in the northwestern portion of the Panama Bight in the Pacific Ocean (Fig. 1). The broodstock was developed in collaboration with the Overseas Fishery Cooperation Foundation (OFCF) of Japan. The design of the seawater system, plus specific details of the capture, handling, and feeding procedures for the broodstock yellowfin tuna are described by Wexler et al. (2003). We began collecting this species in coastal waters in the vicinity of the Laboratory in early 1996, and initially placed 55 individuals in the main broodstock tank (concrete, in-ground, 17 m diameter, 6 m deep) in June and September of 1996. We captured an additional 24 fish in September and October 1996 and maintained them in a smaller (8.5 m diameter, 6 m deep) in-ground tank as a reserve group. The tanks received filtered seawater by intake lines that extended outside Achotines Bay, and both tanks received biological filtration and partial recirculation. The water delivery for the main broodstock tank flowed through an aeration tower (400 m3/h) designed to aerate and degas the makeup and recirculated water entering the tank. We installed several translucent panels in the roof above the main tank to allow exposure to the natural photoperiod. Water temperature, salinity, dissolved oxygen (DO), and oxygen saturation in the tanks were recorded on a daily basis. We measured ammonia, nitrite, nitrate, and carbon dioxide on a weekly or semi-weekly basis.

[2] Masuma, S., N. Tezuka, K. Teruya, M. Oka, M. Kanematsu, and H. Nikaido. 1993. Unpubl. data. Yaeyama Experimental Station, Japan Sea Farming Association, 148 Ohta Ishigaki, Okinawa 907 Japan.

[3] Nakazawa, A. 2004. Personal commun. OFCF (Overseas Fishery Cooperation Foundation), Sankaido Bldg. 9-13, Akasaka 1, Minato-ku, Tokyo 107-0052, Japan.

We fed the broodstock a controlled diet of market squid (*Loligo opalescens*), Argentine shortfin squid (*Illex argentinus*), Pacific thread herring (*Opisthonema* spp.), Pacific anchoveta (*Cetengraulis mysticetus*), and bigscale anchovy (*Anchovia macrolepidota*). The daily ration was usually divided into 50% squid and 50% fish.

Nonlinear least-squares procedures were used to obtain growth parameters for the yellowfin broodstock (Tomlinson[4]) in order to estimate growth rates and sizes at age and length (Wexler et al., 2003).

Spawning

During October 1996, the fish in the main broodstock tank began to exhibit courtship behavior in the late afternoons (see subsection "Spawning behavior"). We began monitoring the broodstock tank for egg production during this time. On 8 October 1996, we collected fertilized eggs in the tank for the first time. The fish spawned sporadically throughout October and November 1996, and by December 1996 were spawning daily. Using the estimated ages of wild yellowfin tuna in the eastern Pacific Ocean (Wild, 1986) and applying them to the lengths and weights of our broodstock fish (Wexler et al., 2003), we estimated the average age of the broodstock fish at the time of first spawning. During 1999–2000, we estimated the spawning periodicity and age at first-spawning of individual females. We compared the mitochondrial DNA genotypes of the female broodstock with those of their offspring (eggs and yolksac larvae) on a weekly basis from August 1999 through August 2000. Mitochondrial DNA analysis was conducted by using polymerase chain reaction/restriction fragment length polymorphism (PCR/RFLP) methods. The genetic analysis is described in greater detail in Niwa et al. (2003).

To determine the time of spawning each day, we checked approximately every 15 minutes for fertilized eggs at the surface of the tank with a hand-held dipnet, usually beginning in mid- afternoon because the fish most often spawned during the late afternoon or evening. Yellowfin tuna eggs, when fertilized, are positively buoyant and rise to the surface in a tank. The time at which eggs were first caught in the dipnet was noted as the "time of spawning." This is a conservative estimate because the fish spawned at different depths and locations in the tank, and we always sampled for eggs at the same location in the tank. We recorded the temperature of the broodstock tank at the time of spawning.

Although we did not anticipate spawning to occur in the reserve tank, the yellowfin tuna began spawning after 7 to 8 months in captivity in mid-April 1997. After the initial spawning in the reserve tank, we monitored the tank daily for fertilized eggs. In October 1997, we collected eggs spawned by the one remaining pair of fish to study Mendelian inheritance of nuclear DNA variants (Chow et al., 2001). We sacrificed the breeding pair after six spawning events and took samples of their muscle tissue for genetic analysis.

Spawning behavior

When the fish spawned before sunset, we made visual observations to describe the courtship and spawning behavior. In addition, we used an underwater video camera connected to a surface video recorder to tape the spawning behavior. On several occasions, we positioned the camera at a depth of 1 to 4 m in different locations and at different angles in the main broodstock tank. The camera recorded continuously for approximately 1 h. We viewed the video tapes and chose footage that showed both courtship and spawning behaviors for behavioral analysis.

Egg collection

In early 1997, we constructed an egg-collection system with three PVC pipes, placed at different depths between the water surface and 70 cm below the surface, so that eggs were siphoned into a square egg-collection basket (1 m × 1 m) made of porous fabric (mesh size 200 μm). We also collected eggs with dipnets and with an egg seine that sampled the entire surface of the tank. In early 1998, we attached a stationary drift net (trapezoidal opening 70 cm height × 20 cm [top width] and 40 cm [bottom width] × 1.6 m long) to one of the siphons to further standardize the egg collections. We considered the siphon system (1997) and the drift net+siphon system (1998–2000) as equivalent sampling systems because the same area in the water column (70 cm × 20 cm) was sampled, siphoned into the same egg collection basket (1 m × 1 m), and sampled daily for the same period.

We collected and counted eggs from each spawning event approximately two hours after the estimated time of spawning. We washed the eggs from the collection basket into a 20-L container. We then set the egg collection basket back into place until the next morning, when we made a second, supplementary collection. We included the second collections in the daily estimates of egg numbers, but these eggs were not used in developmental or experimental analyses.

To determine the number of eggs collected, we brought the egg collection container to 10 L of water volume and lightly agitated the mixture until the eggs were well distributed. We took three 5-mL samples with a wide-mouthed pipette and placed them in three separate, glass counting dishes. We counted the individual eggs in each of the three dishes under a dissecting microscope, calculated the mean, and estimated by extrapolation the total number of eggs in the container. Standardized egg production in the main tank was calculated daily as the number of eggs collected divided by the total biomass of females assumed to be spawning (all those ≥20 kg) in the tank.

[4] Tomlinson, P. 2001. Personal commun. Inter-American Tropical Tuna Commission, 8604 La Jolla Shores Drive, La Jolla, CA 92037.

Determination of egg stage and average egg size

We determined the stage of development of the eggs (egg stage) and measured the egg diameter and oil globule diameter of 30 fresh, randomly selected eggs from each standard collection made at 2 h after fertilization. We measured the eggs to the nearest 0.1 mm with a dissecting microscope fitted with an ocular micrometer. Eggs were classified developmentally according to the terms used by Fritzsche (1978). Egg-stage duration was estimated as the time period from fertilization to 50% hatching (defined below).

Incubation of eggs

We incubated the eggs in conical fiberglass tanks containing 300 L of 1-μm-filtered, UV-sterilized seawater. Through mid-1997, the incubation tanks were exposed to ambient air temperatures and indirect ambient light. Beginning in mid-1997, the incubation tanks were housed in a room with indirect fluorescent lighting and at a constant temperature. The incubation tanks were in total darkness during the night, and were never exposed to direct sunlight or overhead fluorescent light at any time. We used tanks with both flow-through and closed systems for incubation, but we detected no notable differences in hatching success between the two systems. We rinsed the eggs in a 500-μm sieve before placing them in the incubation tanks to eliminate any potentially harmful organisms such as *Benedenia* trematodes or parasitic copepods that might have transferred with the egg sample from the broodstock tank. Beginning in January 1997, we recorded the daily temperatures of the incubation tanks approximately four times between initial stocking and the time of hatching.

Determination of time at hatching

To determine the time at 50% hatching, we collected a sample of eggs from the incubation tank at 15-min intervals, beginning about 12 to 15 h (depending on water temperature) after the estimated time of spawning. When 50% of the eggs in the sample were hatched, we recorded the time. Approximately 2 hours after 50% hatching, we made a final estimate of the mean hatching rate. We took three 300-mL samples from the incubation tank and counted the total number of dead and live eggs and yolksac larvae. Live unhatched eggs, which made up a small portion (<5%) of the samples, were considered to be almost ready to hatch because our experience has shown that the majority of these eggs eventually hatch. The estimated final percent hatching was calculated as

$$\textit{Final \% hatching} = (\textit{no. larvae} + \textit{no. live eggs}) / (\textit{no. larvae} + \textit{no. live eggs} + \textit{no. dead eggs} + \textit{no. dead larvae}) \times 100.$$

Collection of yolksac larvae

After all the larvae were hatched (final hatching), we made morphometric measurements on 20 randomly selected yolksac-stage larvae from each daily cohort. For each larva we measured total length (TL), notochord length (NL), yolk length, yolk height, and oil globule diameter to the nearest 0.1 mm.

Developmental series

Periodically we followed the development of a daily cohort of eggs and larvae from fertilization to first-feeding (normally a duration of 3.5 days). We initiated a developmental series whenever the daily mean temperature of the broodstock tank changed by at least 1°C. Each developmental series entailed sampling eggs at 15-min intervals for the first 4 hours after fertilization, at 1-h intervals for the next 6 h, and then at 2-h intervals until the time at 50% hatching. After final hatching, we sampled yolksac larvae at 6-h intervals until the larvae were ready to feed. We considered a larva to be at first-feeding stage when its retina was pigmented, the alimentary tract was formed, and the mouth was fully developed. We took morphometric measurements on 20–30 fresh eggs and yolksac larvae, as described previously. At first feeding, we measured 20 live larvae for TL, NL, the height and length of any remaining yolk, and the diameter of the oil globule. We measured mouth width on freshly fixed (5% formalin) first-feeding larvae because of the difficulty in obtaining accurate mouth measurements on live specimens.

Dry weights of eggs, yolksac larvae, and first-feeding larvae

For each developmental series examined, we obtained fresh dry weights of 20–30 eggs, yolksac larvae, and first-feeding larvae. We used 8-mm diameter aluminum pans that were dried in an oven at 60°C for 24 h, desiccated for 24 h, and then individually weighed to the nearest 0.1 μg on a microbalance. After measuring, we rinsed the larvae and eggs multiple times with distilled water to remove salts and particulate matter. We placed an individual egg or larva in a preweighed aluminum pan, dried it at 60°C for 48 h, desiccated it for 48 h, and then weighed the specimen to the nearest 0.1 μg.

Data analysis

We analyzed spawning parameters and the characteristics of eggs and early-stage larvae in relation to biological and physical data, including water temperature, time of day, and lunar cycle, from October 1996 through March 2000. We analyzed the relationships of daily ration and female size with egg size and egg production. We considered 20 kg as the minimum size for actively spawning females, based on the size at first-spawning from the genetic analysis (Niwa et al., 2003) and our observations of courtship and spawning behaviors. We

analyzed egg parameters possibly affected by size of females (standardized egg production, egg size) only during the period from June 1997 through July 1999. During this period only the original broodstock group was spawning, and we estimated that the majority of females in the tank were actively spawning (i.e., ≥20 kg each). This eliminated any confounding effects due to newly introduced immature females. Statistical analyses of the data included linear regression, correlation, and multiple regression, and followed the methods of Zar (1984). Statistical programs were run in Microsoft Excel and S-Plus 6.0 (Mathsoft, Inc., Seattle, WA).

Results

The spawning patterns and subsequent egg and larval development are described only for the fish in the main broodstock tank in the first 11 subsections. A short synopsis of the spawning patterns of the fish in the reserve tank is presented in the last subsection.

Broodstock fish

A total of 55 yellowfin tuna were initially stocked in the main broodstock tank in June and September of 1996. At stocking, the fish ranged in length from 51 to 78 cm fork length (FL) (mean of 62 cm FL) and weighed between 3 and 8 kg (mean of 5 kg). The sex composition of the original 55 fish (determined later at death) was 54% female and 46% male. Spawning first occurred in the main broodstock tank on 8 October 1996. At that time, there were 24 females (ranging from 6 to 16 kg and 65 to 93 cm FL) and 20 males (ranging from 6 to 14 kg and 66 to 86 cm FL) in the tank. From observations of courtship behavior during the first 2 to 4 months of spawning, it appeared that only a small group of larger individuals (generally >80 cm FL) was spawning. This pattern changed over time, as more of the broodstock fish attained reproductive size, and by mid-1997 it appeared from the courtship behavior that most of the broodstock fish were participating in the spawning. By mid-1997, there were 19 females (ranging from 13 to 30 kg and 87 to 108 cm FL, averaging 20 kg and 98 cm FL) and 16 males (ranging from 15 to 30 kg and 89 to 112 cm FL, averaging 22 kg and 99 cm FL) in the main tank. Using the estimated ages of wild yellowfin tuna in the eastern Pacific Ocean (Wild, 1986) and applying them to the lengths and weights of our broodstock fish (Wexler et al., 2003), we estimated that the average age of the broodstock fish in mid-1997 was approximately 2 years.

The broodstock population ranged in number from 55 (in September 1996) to five (in July 1999). In mid-August of 1999, we added 14 fish (ranging from 8 to 15 kg and 74 to 89 cm FL) to the main tank to supplement the spawning group. In February of 2000, we added another group of six fish (ranging from 4 to 14 kg and 58 to 71 cm FL) to the tank. The longest time that any individual fish from these broodstock groups survived in captivity was 4.7 years, although average survival in captivity was 1.9 years. Estimated ages of broodstock fish at death averaged 3.1 years and ranged from 1.4 to 6.1 years. Mortalities occurred gradually over time—most often caused by strikes against the tank wall—during the early morning hours before feeding. The average size of the broodstock fish increased over time, and reached a maximum in mid-August 1999. At that time, there were four females (ranging from 46 to 77 kg and 141 to 150 cm FL, averaging 67 kg and 147 cm FL) and one male (50 kg and 133 cm FL) in the main tank. Several of these fish attained sizes >85 kg and 155 cm FL at the time of their deaths in March and October 2000. Estimated growth rates in length for the broodstock fish ranged from 0.9 to 4.0 cm/month and decreased with increasing lengths of the fish. Estimated growth rates in weight ranged from 0.8 to 1.6 kg/ month for fish <19 kg and 1.7 to 1.9 kg/month for sizes >19 kg (Wexler et al., 2003).

Water temperature, spawning, and egg incubation

The mean daily water temperature in the main broodstock tank fluctuated with the ocean temperatures and ranged from 20.1° to 29.7°C, averaging 27.3°C (SD=1.5) (Fig. 2A). Periods of reduced temperatures occurred each year during the coastal upwelling season from January through March. Spawning occurred when the daily mean tank temperature was 23.3° to 29.7°C, and averaged 27.7°C (SD=1.1) at the time of spawning (Fig. 2A). The minimum spawning temperature during most years and seasons was about 24.0°C. The daily mean water temperature decreased to 24.0°C or below during three of the four years of the study; however, only two spawnings occurred at mean temperatures below 24.0°C. During most years, spawning occurred daily and continuously for several months, but spawning ceased when tank temperatures decreased below 24°C (March 1997, March 1999, and February 2000) or decreased by at least 0.5°C for at least one week (December 1997, October 1998, and August 1999). The cessation of spawning in October 1998 extended for 5.5 months. During this period, water temperatures were sufficient for spawning, although they were steadily decreasing (from 28°C to <24°C) during most of the period.

The mean water temperatures in the egg incubation tanks ranged from 21.9° to 29.8°C, averaging 27.6°C (SD=1.0) (Fig. 2B). The pattern of incubation temperatures closely paralleled the pattern of mean daily water temperatures for the main broodstock tank, although the incubation temperatures did not decrease as much as those of the main broodstock tank during the upwelling period in early 1997 (because of the influence of higher air temperatures on the incubation tanks). From January 1997 through March 2000, incubation temperatures and the broodstock tank temperatures were highly correlated (r=0.74, df=886, P<0.001), and we considered the two data sets as equally representative of water temperatures observed in the laboratory.

Seawater characteristics and spawning

Spawning in the main broodstock tank occurred at salinities of 26 to 36 ppt, but during most months salinities ranged from 30 to 34 ppt. Dissolved oxygen ranged from 65% to 107% of saturation but usually exceeded 80% of saturation. The seawater pH ranged from 7.6 to 8.3, and ammonia was always below detection levels. During periods of cessation of spawning, salinities were generally stable between 30 and 34 ppt, and dissolved oxygen, pH, and ammonia were also within normal ranges.

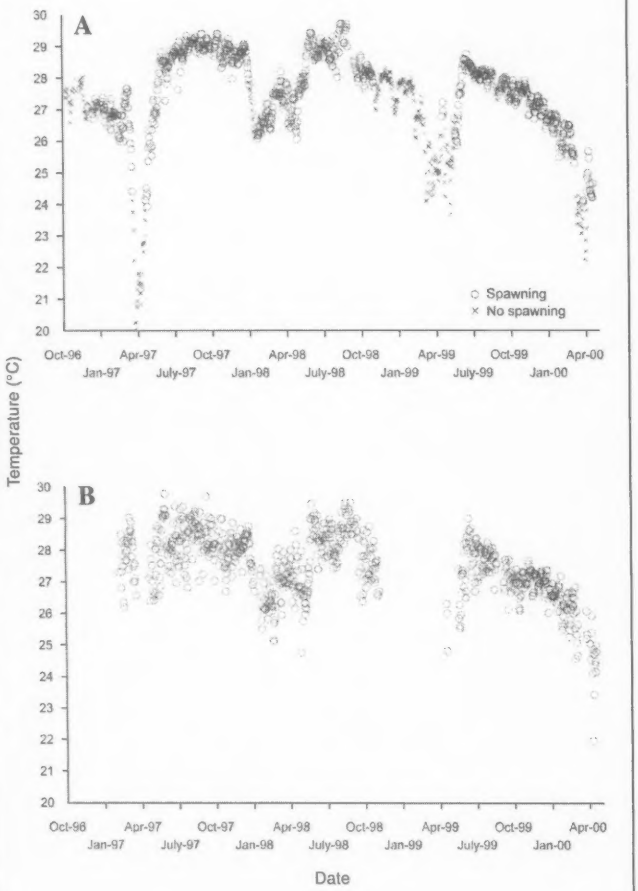


Figure 2

Mean daily water temperature in (**A**) the main broodstock tank, and (**B**) the incubation tanks from October 1996 through March 2000. In (A), plotted symbols are individual dates on which there was either spawning (indicated by o) or no spawning (indicated by x). In (B), plotted symbols are individual dates on which egg incubation occurred.

Courtship and spawning behavior

The daily courtship and spawning behavior of the broodstock fish followed a consistent pattern. Courtship behavior usually began in the afternoon, and spawning occurred most often in the late afternoon or evening. The courtship behavior was usually initiated with a loose aggregation by most of the fish in the central, bottom area of the tank, although at times some pairing behavior was observed before formation of the aggregation. Smaller groups of fish (two to five individuals per group) would break off from the main aggregation and exhibit courtship behavior that included paired swimming, chasing, and bursts of speed throughout the tank. The paired swimming and chasing was often in the pattern of loops throughout the water column. A courtship group consisted of a single fish, presumed to be a female, followed closely by one to three fish, assumed to be males. During the courtship process males would often flash vertical bars (also termed feeding bars by tuna biologists) along the sides of their bodies. Fish presumed to be females would often release concentrated discharge trails from their vents during the late stages of courtship. Courtship behaviors would continue unabated for 1 to 4 h prior to actual spawning.

Two to eight spawning groups would eventually break off from the courtship aggregation and spawning would take place nearly simultaneously in the tank. When the fish spawned, they would typically swim in an ever-tightening circle—one female in front and one to five males following closely behind in single file. During actual spawning we always observed the trailing individuals releasing milt. As the females in each group began to release their eggs, they would tighten their swimming circle and the males would do the same while they released milt. This action resulted in the entire spawning group swimming in a very tight circle, which appeared to facilitate the mixing of eggs and milt. During spawning, the swimming speeds of the fish usually decreased, compared to the speeds during courtship, but at times swimming would remain quite rapid while eggs and milt were released. The fish within spawning groups moved horizontally as they spawned, but the fish often added some vortex-like movement upward through the water column as spawning occurred. Within each group, spawning was usually completed within 30 to 45 sec. The entire spawning event was often finished within 60 to 90 sec, although at times spawning events would continue for up to 5 to 10 min.

Spawning periodicity and size and age at first-spawning

The yellowfin tuna broodstock spawned 963 times, at almost daily frequencies, over the study period, although not all the fish were sexually mature during the entire period. Genetic analysis of female broodstock and their eggs and larvae (Niwa et al., 2003) corroborated our observations and videotape analysis of courtship and spawning behaviors and spawning frequencies. The mitochondrial DNA analysis confirmed that multiple females were contributing to individual spawns over protracted time periods (weeks to months). From August 1999 through August 2000, there were ten identified females in the tank. We identified up to six female genotypes in egg or larval samples on individual spawning dates, and we observed the same genotypes for at least five females on successive sampling dates over 1 to 3 months. The spawning frequencies estimated by this analysis were undoubtedly conservative because the sampling was not conducted every day, even though spawning was occurring daily.

When spawning first occurred (8 October 1996), we estimated that the average age of the broodstock females was 1.6 years (range 1.3–2.0 years, n=24). For the 1999–2000 period, we estimated that the weight of a female at first spawning was 12 to 28 kg and its size was 75 to 112 cm FL. These measurements correspond to an average age of 2.0 years (range 1.6–2.8 years, n=7), where the majority of females would be slightly younger than 2.0 years.

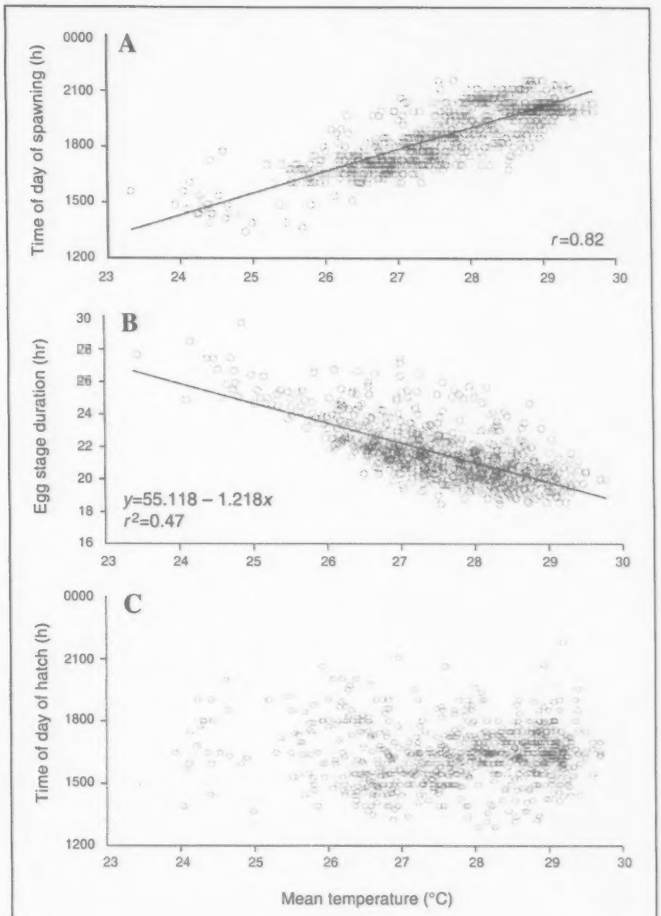


Figure 3

The relationship between mean daily water temperature and (**A**) time of day of spawning, (**B**) egg-stage duration, and (**C**) time of day of hatching for yellowfin tuna (*Thunnus albacares*) in captivity. Plotted values are daily estimates.

Timing of spawning and hatching

The time of day that spawning occurred ranged from 1330 to 2130 h, and was most frequent between 1600 and 2100 h (Fig. 3A). The time of day of spawning was strongly and positively correlated (r=0.82, df=937, P<0.001) with mean daily water temperature. For example, at mean daily water temperatures of 25°C or below, spawning occurred in the afternoon between 1330 h and 1745 h. At temperatures near 27°C, spawning took place near 1800 h, and at water temperatures of 27.5°C or above, spawning occurred at night between 1845 h and 2130 h.

Egg-stage duration was inversely related to mean incubation temperature (Fig. 3B). Mean egg-stage duration ranged from a maximum of 28 h at 24°C to a minimum of 18 h at 29°C or above. The relationship was best described by a highly significant linear regression (r^2=0.47, df=827, P<0.001).

Water temperature imposed opposite effects on the time of day of spawning (direct relationship) and egg-stage duration (inverse relationship), and the net effect of these relationships was a narrow range for the time of day at hatching (Fig. 3C). Over the 3.5-yr study period, the eggs hatched between 1300 h and 2145 h. However, over 95% of the hatch times occurred in a narrow time frame between 1500 h and 1900 h, regardless of water temperature.

Egg production and daily ration

For the original broodstock group, there was no definitive relationship between standardized egg production and mean size of spawning females, nor was there a significant overall correlation between standardized egg production and daily ration over the entire study

period (r=0.15, df=564, P>0.10). However, over short time periods (<1 month), the spawning females increased their egg production in response to short-term increases in daily ration. Over the period of June 1997 through July 1999, we varied the daily ration of food for the broodstock fish from approximately 1.0% to 4.5% body wt/day. During eight periods, we purposely increased daily food ration from 9% to 33% over time durations of 3 to 14 days. The rations were usually increased in response to greater food requirements, signaled by increasing feeding activity, or in attempts to effect increased egg production. During all eight of these periods, the standardized egg production in the tank increased from 30% to 234% (Fig. 4). There was a time lag until peak egg production occurred (indicated by numbers in parentheses in Fig. 4) after the initial increase in ration. Egg production increased, and peaked from 4 to 21 (average of 12) days after the introduction of increased rations. The percentage increase in egg production tended to be greater with greater increases in daily ration, but the relationship was not significant (r=0.36, df=7, P>0.10). The increases in egg production occurred over a range of water temperatures from 27.3° to 29.4°C; however, there was no clear association between water temperature and standardized egg production.

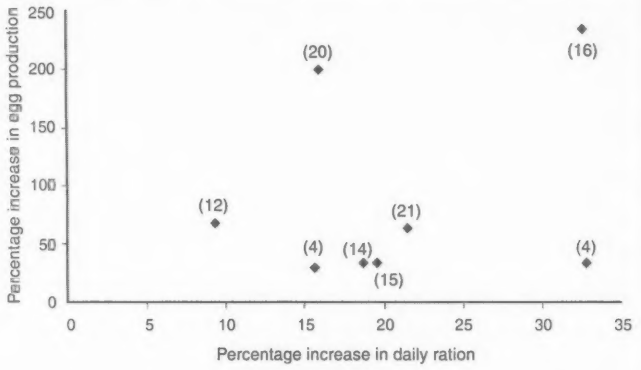


Figure 4

Increases in egg production by female yellowfin tuna (*Thunnus albacares*) broodstock during eight periods of planned increases in daily ration. Each period is represented by a plotted symbol. For each period, the value in parenthesis is the elapsed number of days from the initial increase in ration until the peak egg production was observed.

Spawning and photoperiod

Given the tropical latitude of the Achotines Laboratory (7°25′N), photoperiod was relatively constant during the study. From October 1996 through March 2000, day length varied by only 53 min, and changed by only 3 to 12 min/month (U.S. Naval Observatory Astronomical Applications Database[5]). No strong relationships between either frequency of spawning or standardized egg production and photoperiod were apparent. Cessations in spawning associated with short-term decreases in tank water temperature (in December 1997, October 1998, and August 1999) occurred during periods of decreasing photoperiod, while cessations in spawning due to water temperature decreases below the apparent-minimum for spawning (<24°C) (in March 1997, March 1999, and February 2000) occurred during periods of increasing photoperiod.

Spawning and lunar phase

Spawning occurred almost daily and showed no definitive relationship with lunar phase on a daily or monthly basis. Also, there was no significant correlation between standardized egg production and lunar phase (r=0.10, df=564, P>0.20). In each of the 26 months for which standardized egg production was calculated (June 1997 through July 1999), the monthly maxima egg production occurred equally during the first two quarters (new moon to half-moon) and last two quarters (half-moon to full moon) of each lunar cycle. However, over the 2-year period, the maximum egg production from individual spawns occurred most often at greater illumination phases of the moon. Of the 20 spawns with the greatest standardized egg production, 90% occurred during the third or fourth quarters (i.e., half-moon to full-moon), although only one of these 20 spawns occurred directly on a full moon.

Egg-stage duration and egg size

Egg-stage duration increased with larger egg size, although the predictive power of the linear regression was low (r^2=0.09, df=837, P<0.001). Water temperature, as presented previously (Fig. 3B), exhibited a strong inverse relationship with egg stage duration. We used stepwise regression to build a model to predict egg-stage duration as a function of egg size and temperature:

$$Y = 27.96\ (\pm 1.69\ \mathrm{SE}) + 29.05\ (\pm 1.55)\ D - 1.28\ (\pm 0.04)\ DT \quad (r^2=0.58,\ \mathrm{df}=826,\ P<0.001),$$

[5] U.S. Naval Observatory Astronomical Applications Database. 2002. Table of sunrise/sunset, Astronomical Applications Dept., Data Services. Website: http://aa.usno.navy.mil/data (accessed August 2002).

Table 1

Morphometric measurements and dry weights of eggs, yolk-sac larvae, and first-feeding larvae of yellowfin tuna (*Thunnus albacares*).

Eggs	Egg diameter (mm)	Oil globule (mm)	Weight (μg)
Mean	0.97	0.22	42.8
Standard error	<0.01	<0.01	0.4
Minimum	0.85	0.15	33.6
Maximum	1.13	0.28	59.7
n	27,343	27,359	197
Yolksac larvae	**Total length (mm)**	**Notochord length (mm)**	**Weight (μg)**
Mean	2.61	2.51	30.1
Standard error	<0.01	<0.01	0.4
Minimum	2.10	2.00	25.0
Maximum	3.6	2.90	40.8
n	15,832	15,849	132
First-feeding larvae	**Total length (mm)**	**Notochord length (mm)**	**Mouth width (mm)**	**Weight (μg)**
Mean	3.49	3.32	0.262	21.7
Standard error	<0.01	<0.01	<0.01	0.4
Minimum	2.90	2.70	0.225	13.8
Maximum	4.10	3.90	0.350	29.6
n	272	272	126	105

where Y = egg stage duration (h),
D = mean egg diameter, and
T = mean incubation temperature (°C).

The diameter of individual fertilized eggs ranged from 0.85 to 1.13 mm and averaged 0.97 mm (Table 1). Each egg contained a single oil globule that averaged 0.22 mm in diameter. The dry weight of individual eggs ranged from 34 to 60 μg and averaged 43 μg (Table 1). Mean daily egg diameter was inversely related to water temperature during the period when the original broodstock (stocked in 1996) were spawning (Fig. 5A; df=892, $P<0.001$), although there was considerable scatter about the regression ($r^2=0.23$). Mean egg diameter was significantly correlated ($r=0.45$, df=553, $P<0.001$) with the mean weight of spawning females (all females ≥20 kg) in the original broodstock group (Fig. 5B).

Larval size at hatching and hatching success

At hatching, the larvae averaged 2.5 mm NL (range 2.0–2.9 mm NL; SD=0.16) (Table 1). Larvae at hatching had unpigmented eyes, no alimentary tract nor mouth, and exhibited a large, elliptical yolk mass containing a single posterior oil globule. The dry weight of individual larvae at hatching ranged from 25 to 41 μg, averaging 30 μg (SD=4) (Table 1). Mean larval length at hatching was positively correlated ($r=0.46$, df=498, $P<0.001$) with mean egg diameter (Fig. 6A), and negatively correlated ($r=-0.27$, df=774, $P<0.05$) with mean incubation temperature (Fig. 6B).

The percentage hatching of eggs spawned in captivity ranged from 9.5% to 99.0% and averaged 83% (SD=14.7%). In general, the hatching success was high, with over 84% of the hatchings occurring at rates >70%. The percentage hatching showed no relationship with either water temperature or larval length.

Egg and early larval development

Yellowfin tuna egg development was rapid. The developmental duration from fertilization to hatching followed a curvilinear pattern (Fig. 7), and the egg-stage duration was temperature dependent (Fig. 3B). At a modal incubation temperature of 27.0°C, egg-stage duration was 21.65 h (Fig. 7). At 27.0°C, cell cleavage occurred <1 h after fertilization, early embryo gastrulation occurred about 6 h after fertilization, the embryo first formed after 8 h of development, and the embryo was in the tail-free stage approximately 17 h after fertilization. The specific gravity of fertilized eggs changed with development. Upon fertilization, eggs were positively buoyant and would rise to the surface neuston layer of the broodstock tank. Eggs remained positively buoyant into the tail-free stage, but 2 to 4 h (dependent on temperature) before hatching the specific gravity changed and the eggs became negatively buoyant until they hatched. The nega-

tive buoyancy in the late egg stage was observed at all salinities at which incubation occurred (26 to 36 ppt).

The duration of the yolksac larval stage was inversely (but weakly) related to temperature and ranged from 56 h at 29.0°C to 65 h at 23.5°C. Eye pigmentation and mouth formation in larvae occurred almost simultaneously, and at the stage of mouth formation there was usually only a trace of yolk remaining. First-feeding larvae averaged 3.3 (SD =0.18) mm NL (range 2.7–3.9 mm) and weighed between 14 and 30 μg (average 22 μg) (Table 1). The mouth width of first-feeding larvae ranged from 225 to 350 μm, averaging 262 μm (Table 1).

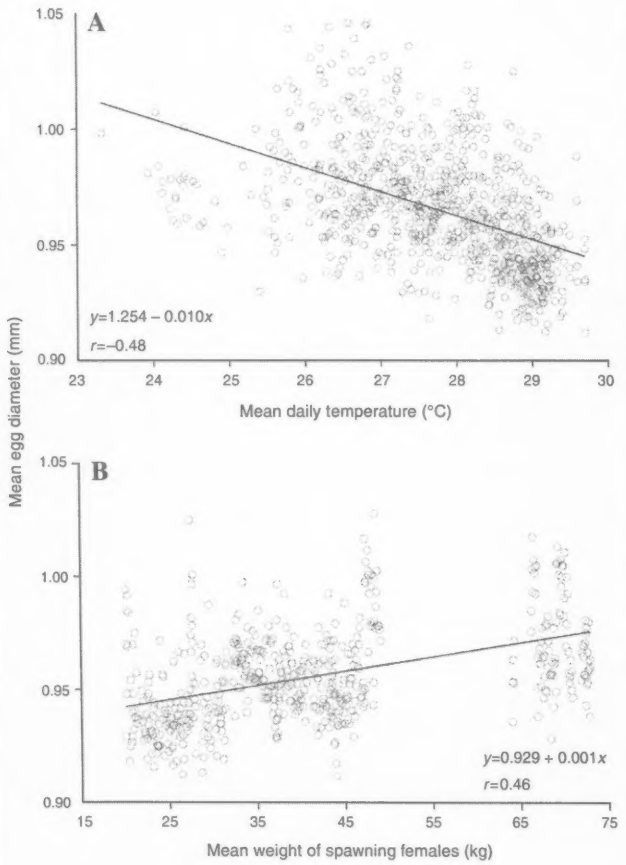


Figure 5

(**A**) The relationship between mean egg diameter and mean daily water temperature, and (**B**) the relationship between mean egg diameter and mean weight of spawning females of yellowfin tuna (*Thunnus albacares*) in captivity.

Spawning in the reserve tank

The fish in the smaller reserve tank began spawning in mid-April 1997. At that time there were four females and four males in the tank. When spawning first commenced, the females ranged from approximately 7.0 to 10.5 kg (average 9 kg) and 70 to 74 cm FL (average 72 cm), while the males ranged from 5.5 to 9.0 kg (average 7.5 kg) and 62 to 74 cm FL (average 66 cm). We did not determine how many fish were involved in the initial spawning, but it appeared from courtship behavior that only a few of the larger individuals were participating in spawning during the first 1 to 2 months. Spawning continued into October 1997, when we sacrificed the one remaining pair of fish. At the time of death, the female was 16 kg and 94 cm FL and the male was 12 kg and 79 cm FL. We did not monitor the numbers or characteristics of eggs or larvae in the reserve tank. Spawning in the reserve tank occurred over a water temperature range of 24.4° to 29.2°C.

Discussion

The spawning by the yellowfin tuna broodstock at the Achotines Laboratory, beginning in 1996, represents the first occurrence worldwide of sustained spawning by yellowfin tuna in landbased facilities. Over 3.5 years, the broodstock fish spawned in our large broodstock tank (1362 m^3) at near-daily frequencies over extended time periods. In general, the fish spawned as long as they received adequate daily rations of food and the water temperature was 24°C or higher. The reserve group also spawned for a 6-month period in a tank of reduced volume (270 m^3).

Courtship and spawning behaviors

No courtship behavior or spawning aggregation has ever been observed in tunas in nature. The sustained spawning by the yellowfin tuna broodstock in this study allowed us to observe and analyze reproductive behavior that has not been described previously. The courtship and spawning behavior of the captive yellowfin tuna was ritualized and consistent among three groups of broodstock fish over almost four years. The courtship behavior (chasing by males, paired swimming) always occurred after the initial formation of a central aggregation of participating fish. During the actual spawning events, males were not monogamous to single spawning groups and would often move from

one spawning female to another. Spawning behavior (swimming in tightening circles with females in the lead position) ensured that eggs and milt would be well mixed. Most spawning groups moved over a range of depths in the broodstock tank, so it is likely in nature that yellowfin tuna in spawning groups move vertically to some degree during release of gametes.

The aggregations and courtship behavior usually occurred unabated for several hours before spawning and represented a significant energetic investment by the broodstock fish. The daily energetic cost of maturing a batch of eggs for a single spawning by yellowfin tuna sampled at sea was estimated at 1.06% of body weight by Schaefer (1996), but that estimate did not include the energetic costs of courtship or spawning behavior. If the behavior of our captive spawning group is representative of yellowfin tuna behavior in nature, then we believe that yellowfin tuna in the wild probably form large spawning aggregations and individual fish may invest considerable time (1 to 4 h) and energy (costs unknown) on daily courtship and spawning activities.

The behavior of the yellowfin tuna broodstock is predictable on a daily basis, which would indicate that a synchronization mechanism is inherent to the behavior. Most of the courtship and spawning behavior of the fish appeared to be driven by female behavior (i.e., females led, males followed). In teleost fishes, the release of eggs and milt during spawning is synchronized by the release of pheromones, predominantly by females (Liley et al., 1991). Sex hormones and hormone metabolites are water soluble and indicate the sender's reproductive status. Pheromones studied to date appear to be of two types, steroids and prostaglandins, and they are released by females in concentrated urine trails (Stacey, 1984, 1991). Female yellowfin tuna in our spawning group often released discharge trails during the courtship process just before spawning, and at times we misinterpreted these trails as egg emissions. Given the ritualized nature of the courtship and spawning behavior of both sexes in our broodstock, most of the discharge trails during late-courtship may have been pheromone releases by the females, although future confirmation with biochemical or immunoassay analyses would be required.

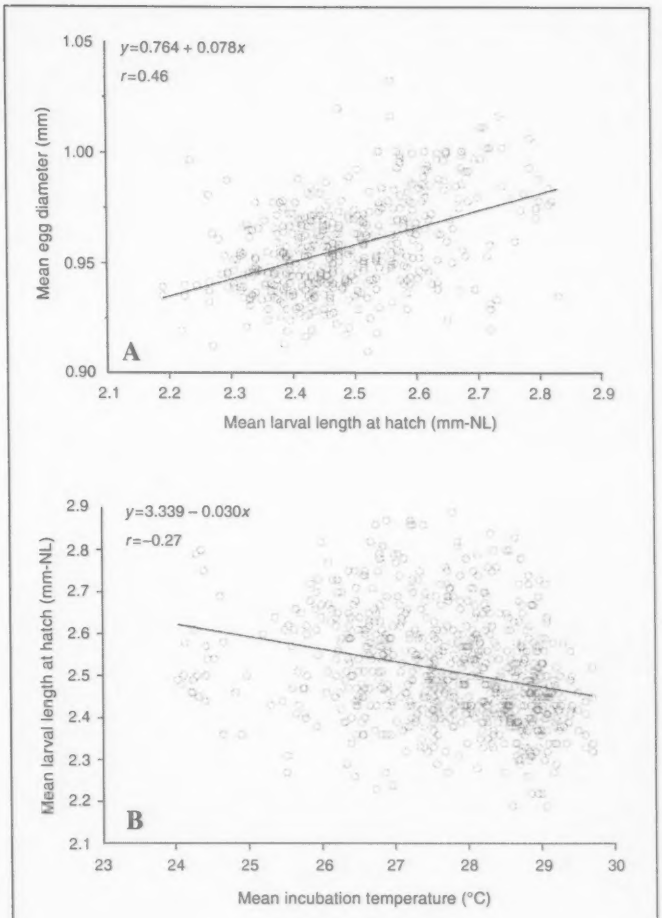


Figure 6

(**A**) The relationship between mean larval length at hatching and mean egg diameter, and (**B**) the relationship between mean larval length and mean incubation temperature for yellowfin tuna (*Thunnus albacares*) in captivity.

Diel patterns of spawning and egg hatching

The diel timing of spawning by the broodstock yellowfin tuna was finely tuned to water temperature and, combined with the strong inverse relationship between water temperature and egg duration, resulted in a predictable and narrow range in the time of hatching. The majority of spawning occurred after sunset and at higher (generally >27°C) water temperatures. However, when water temperatures decreased, the broodstock fish spawned earlier in the day. This temporal shift resulted in nearly all hatching occurring in the late afternoon or early evening. We believe that this pattern for the diel timing of spawning and hatching is important and has adaptive significance for the early life history of yellowfin tuna. In nature, the maintenance of a conservative time for egg hatching would ensure that newly hatched yellowfin larvae spend the first 12 to 15 h after hatching in dimming light or darkness. Because yolksac larvae of marine

fishes are vulnerable to predation by planktivorous fishes and invertebrates (Bailey and Houde, 1989), minimizing the amount of time spent in daylight appears to be a mechanism for maximizing survival for yolksac larvae.

This temporal pattern of hatching would also minimize the exposure of yellowfin tuna yolksac larvae to the ultraviolet effects of sunlight. Although the vertical distribution of yellowfin tuna yolksac larvae in the ocean has not been described, feeding-stage larvae of yellowfin tuna are found predominantly in the upper mixed layer (Leis et al., 1991; Boehlert and Mundy, 1994). The deleterious effects (mostly genetic damage) of ultraviolet radiation are strongest in the upper mixed layer and may affect yolksac larvae more than other early life stages of marine fishes (Vetter et al., 1999). Thus, any adaptation that reduces the amount of time yellowfin tuna yolksac larvae spend in daylight increases their chances of survival.

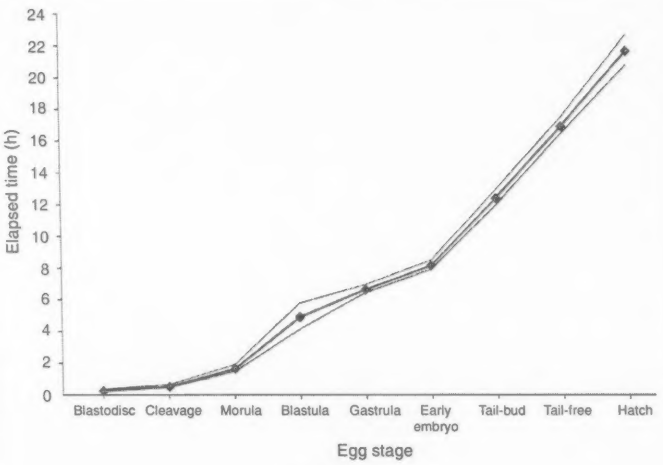


Figure 7

The development of yellowfin tuna (*Thunnus albacares*) eggs from fertilization to hatching at 27°C. Plotted values are mean hours elapsed to reach specific developmental stages. Error envelopes are ±2 SEs.

Most tunas are reported to be nocturnal spawners, according to histological analyses of the ovaries of adult fishes caught at sea (McPherson, 1991; Nikaido et al., 1991; Schaefer, 1998, 2001a). Our experimental results indicate that the view that yellowfin tuna spawn exclusively at night should be reconsidered. The assumption of nocturnal spawning by tunas in past studies has been based on histological analyses of oocyte development and new postovulatory follicles in the ovaries of adult fishes in the wild (collected predominantly at sea surface temperatures >27°C), but the actual water temperatures encountered by the fish before and during spawning were not known. Our results indicate that yellowfin tuna respond to variations in water temperature by altering their time of spawning and that the diel changes in spawning time are precise and predictable. The ability to control the timing of spawning by adults may be mediated by the timing of the release of sex hormones and maturation processes in response to water temperature. It is possible that our results are simply an artifact of captivity because our broodstock fish were confined to a tank and not able to thermoregulate by changing water depth or location as wild fish can. However, we believe that our experimental evidence for the control of the timing of spawning by yellowfin is compelling. The adaptive significance of this spawning pattern is most likely related to the ultimate effects of temperature on development rates of eggs and yolksac larvae (i.e., maintenance of a consistent time of hatching to maximize early larval survival). In the only other similar study on tunas, Miyashita et al. (2000a) reported that cultured bluefin tuna also spawned predominantly before sunset. Daily mean water temperatures in their 4-yr study ranged from 21.6° to 29.2°C, and the mean temperatures during the spawning season ranged from 23.6° to 27.0°C.

Spawning cues

Spawning substrate, food availability, water temperature, photoperiod, and lunar cycle can strongly influence many functions of the teleost reproductive system (Bye, 1984; Stacey, 1984). We consider each of these potential cues for reproduction in yellowfin tuna

Because yellowfin tuna are pelagic spawners, they have no specific substrate requirements. The yellowfin tuna in our study received controlled daily rations to fuel daily spawning costs (Wexler et al., 2003). Under the nonlimiting food conditions that we provided, no relationship was apparent between spawning occurrence and food abundance. However, this pattern of spawning in captivity does not rule out the possibility that the timing of yellowfin tuna reproduction in tropical or subtropical waters could be influenced by seasonal fluctuations in food abundance, such as those associated with seasonal upwelling. Some species of tropical and subtropical marine fishes exhibit reproductive cycles that coincide with periods of upwelling or increased productivity and food availability (Bye, 1984). Tunas in tropical regions usually spawn year-round, but those occurring in the subtropics exhibit seasonal spawning patterns (Fritzsche, 1978; Schaefer, 1998), whereas bluefin tuna and albacore migrate to warm waters to spawn in distinct areas during restricted periods (Collette and Nauen, 1983). Our yellowfin tuna broodstock

did not exhibit any patterns of spawning occurrence that were related to food abundance in captivity (but see the following subsection on "Egg production and daily rations").

Our focus on the processes controlling maturation and spawning of captive yellowfin tuna has centered on the influences of water temperature, photoperiod, and lunar cycle. Water temperature appeared to provide the main exogenous control over the occurrence and timing of spawning of captive yellowfin tuna. The fish spawned over a range of daily mean temperatures from 23.3° to 29.7°C. Spawning occurred at daily mean temperatures <24°C on only two out of 963 dates (single spawning events at 23.3° and 23.9°C), and spawning became intermittent or ceased within 24 hours after those two dates. This thermal range for spawning of yellowfin tuna is similar to that reported from collections at sea of reproductively active adults (Schaefer, 1998) and early-stage larvae (Nishikawa et al., 1985; Boehlert and Mundy, 1994; Lauth and Olson, 1996). In general, tunas spawn at water temperatures ≥24°C (Collette and Nauen, 1983), although larvae of bullet or frigate tunas (or larvae of both) (*Auxis* spp.) and skipjack tuna have been collected at sea at temperatures near 22°C (Richards and Simmons, 1971; Boehlert and Mundy, 1994). In their study of spawning of captive bluefin tuna in Japan, Miyashita et al. (2000a) reported spawning temperatures from 21.6° to 29.2°C.

This study is the first to investigate the relationship on a daily basis between water temperature and spawning by yellowfin tuna over a protracted period. Our results indicate that the sensory ability of yellowfin tuna to detect ambient water temperature and the associated feedback mechanisms involved in neuroendocrine control of ovulation and spawning behavior are rapid and characterized by subdaily response times. Spawning usually ceased within one day after water temperatures decreased by only 0.1 to 0.2°C, and usually recommenced in less than one day after similar minute changes in water temperature. The broodstock altered the time of day of spawning predictably in relation to water temperature, but this behavioral change in the time of day of spawning occurred only after several days of exposure to changes in water temperature. Maturation and spawning in female fishes, in particular the initiation of vitellogenesis, oogenesis, and ovulation, is under hormonal control (Goetz, 1983). Sensory inputs to neuroendocrine control of reproduction include information on external water temperature transmitted via temperature-sensitive afferent nerve fibers (Van der Kraak et al., 1998). The spawning periodicity of the broodstock and their ability to adjust the time of day of spawning in response to water temperature indicate that yellowfin tuna have the ability to rapidly integrate sensory information on water temperature and, often within hours, adjust the hormonal control of final maturation processes and spawning.

Our analysis of spawning by the yellowfin tuna broodstock did not indicate a strong influence of lunar cycles on the timing of spawning or egg production within monthly periods. We originally anticipated some lunar periodicity to spawning because many tropical marine species exhibit lunar spawning rhythms that usually peak around the new moon or full moon (spring tides) (Johannes, 1978; Bye, 1984). Peak spawning on new or full moons in the tropics may be an adaptation to maximize offshore transport of eggs and larvae by spring tides away from increased predation pressure in coastal habitats (Johannes, 1978). Our captive yellowfin tuna, however, were exposed only to lunar cycles in captivity, but not to tidal influences. The mean daily egg production from individual spawnings in our study was highest during phases of greater lunar illumination. This trend in egg production could be viewed as evidence that yellowfin tuna increase their spawning efforts just prior to full moons, but the trend from our data is not definitive. Although adult yellowfin tuna in nature sometimes aggregate around islands and seamounts (Boehlert and Mundy, 1994), spawning by yellowfin tuna is widespread throughout the tropical and subtropical oceans (Nishikawa et al., 1985). Because yellowfin tuna often spawn in pelagic open-ocean habitats, they may not require the same level of synchronization with lunar cycles to aid in egg and larval dispersal as that required by coastal tropical species.

Photoperiod is an important environmental cue for spawning in temperate fish species (Lam, 1983). However, in the tropics, photoperiod hardly varies throughout the year and is usually not a major factor in the control of maturation and spawning of tropical fishes (Lam, 1983). Photoperiod changed very little during our study, and the yellowfin tuna broodstock showed no detectable responses to slight changes in day length.

Egg production and daily rations

Yellowfin tuna in this study exhibited the ability to boost egg production in response to periodic increases in daily food rations. Egg production peaked over periods of 1 to 3 weeks (average 12 days) after food rations were increased. These increases in daily egg production sometimes exceeded 200%, providing strong evidence that yellowfin can convert peaks in exogenous energy consumption into higher egg production in a matter of days or weeks. The adaptive significance of this reproductive pattern is obvious. The ability to increase egg production in response to greater food abundance in oceanic habitats would provide yellowfin tuna with the opportunity to exploit patchy food resources and periodic increased production that can occur in the vicinity of islands, seamounts, and in coastal or equatorial upwelling zones. Results from several field studies, where the abundance of tuna larvae was examined, support our laboratory results. Boehlert and Mundy (1994) suggested that increased abundance of *Thunnus* spp. larvae on the leeward side of Oahu, Hawaii, may be related to greater forage for adult tunas in that region. Lauth and Olson (1996) reported peak abundance of *Euthynnus lineatus* and *Auxis* spp. larvae during periods of peak seasonal upwelling and secondary production in the Panama

Bight, and they suggested that spawning adult tunas may increase batch fecundities in response to greater forage.

Yellowfin tuna are multiple-spawning fish, and their fecundity is not fixed at the beginning of any spawning period (Schaefer, 2001a). Batch fecundity of yellowfin tuna can vary annually or geographically (Schaefer, 1998), although information on daily patterns in batch fecundity of tunas is lacking. Wootton (1979) reported one of the few studies to demonstrate a positive relationship between batch fecundity and daily food ration in nonscombrid species. Our results with captive yellowfin tuna agree with Wootton's data and indicate that over short time periods yellowfin tuna can boost egg production in response to increased food abundance.

Size and age at first spawning and sex ratios

Our estimates of the range of sizes at first spawning for our female yellowfin tuna in 1999–2000 (12 to 28 kg, 75 to 112 cm FL) (Niwa et al., 2003) are not directly comparable to estimates from some studies of wild yellowfin tuna because of slight differences in the reproductive conditions measured. We estimated size at first spawning, whereas estimates from studies of wild fish have included estimates of size at maturity and size of reproductively active fish. Size at maturity, although related to size at first-spawning, is a more conservative estimate than size at first-spawning and does not indicate true reproductive activity. Schaefer (1998) reported that the minimum length of reproductively-active wild fish observed in the eastern Pacific Ocean was 60 cm FL. Fifty percent of the fish in that study were mature at 92 cm FL, and the portion spawning per day at that size was 0.61. McPherson (1991) estimated that the mean length at maturity of yellowfin tuna in the western Pacific Ocean was 108 cm FL. In general, the sizes of reproductively active fish reported for wild yellowfin tuna are comparable to our estimates of size at first spawning. Also, Schaefer's (1998) estimate of 92 cm FL as the length at 50% maturity for wild fish is similar to the average length of our broodstock fish in mid-1997, when we estimated that most of our fish appeared to be spawning.

It appears that the majority of our broodstock began spawning at slightly earlier ages than did the wild yellowfin tuna. Schaefer (1998) estimated the age at first maturity of yellowfin tuna in the eastern Pacific Ocean to be approximately 2 years. Our estimates of age at first spawning for the original broodstock fish ranged from 1.3 to 2.0 years, and averaged 1.6 years, and the estimated age at first spawning for the 1999–2000 females ranged from 1.6 to 2.8 years and averaged 2.0 years. However, the majority of these females were estimated to be slightly younger than 2 years. The more precocious spawning by most of the captive fish was most likely due to greater food rations and higher growth rates compared to those of wild fish during the first 1–2 years in captivity. Our results indicate that fish size, rather than age, is the best predictor of reproductive status of yellowfin tuna.

The sex ratio of the original group of yellowfin tuna in this study was initially 1.2:1.0 (female:male), and females remained slightly more abundant in the spawning group over 3.5 years. A dominance by males in larger length classes has been reported for wild yellowfin tuna, and has been attributed to potential differences in natural mortality rates between the sexes (Suzuki, 1994; Wild, 1994). We saw no evidence of greater mortality in larger females in our broodstock group. However, mortality rates in captivity are expected to be less than in nature because food is not limiting and predators are absent.

Egg and larval development

Yellowfin tuna eggs and newly hatched larvae are morphologically typical of marine pelagic fishes. Fertilized yellowfin tuna eggs average about 1 mm in diameter, and the larvae hatch at a relatively small size (ca. 2.5 mm SL). The weight data that we present in this study are either the first (yolksac larvae, first-feeding larvae) or second (eggs) published estimates for tuna. Yellowfin eggs weigh about 43 μg dry, and weight loss occurs during the embryonic phase, and larvae lose about 33% of the original total weight at hatching and almost 50% of the original weight at first-feeding. The weight loss is due to utilization of yolk and oil during the egg and yolksac stages.

Scombrid early life history is characterized by high mortality rates, high metabolic rates, and exponential growth (Davis et al., 1991; Margulies, 1993; Wexler et al., 2001). Yellowfin tuna larvae at first feeding are intermediate in size (3.3 mm SL, 22 μg in this study) compared to other scombrid larvae (Tanaka et al., 1996), and they exhibit a large scope for growth as juveniles (Kaji et al., 1999; Wexler et al., 2007). Given the low initial weights of yellowfin eggs and yolksac larvae and the high growth rates of larvae and early-juveniles, the potential for weight gain from the egg stage to the stage at first-recruitment for yellowfin (30 cm FL, 6 months of age, IATTC[6]) is very high and approaches a gain in weight from $\times 10^6$ to $\times 10^7$.

Water temperature influences almost every aspect of the egg and yolksac larval stages of yellowfin tuna. Water temperature is inversely related (significantly) to egg size, egg-stage duration, larval size at hatching, and yolksac larval duration. Inverse developmental relationships between water temperature and the sizes and durations of egg and yolksac stages are common in marine fishes (Blaxter, 1969) and have also been reported for cultured bluefin tuna (Miyashita et al., 2000a, 2000b). These inverse relationships are most likely the result of slower responses of ontogenetic pro-

[6] IATTC (Inter-American Tropical Tuna Commission). 2000. Annual report of the Inter-American Tropical Tuna Commission, 1998, 357 p. 8604 La Jolla Shores Drive, La Jolla, CA 92037.

cesses to lower water temperature during oogenesis and embryonic stages (Chambers, 1997). At lower water temperatures, the durations of developmental stages are longer, and eggs and hatched larvae are larger.

An interesting aspect of egg development in yellowfin tuna is the change in buoyancy as the eggs develop. Fertilized eggs are positively buoyant throughout development until a few hours before hatching, when they become negatively buoyant. We assume that the onset of negative buoyancy occurs as the chorion of the egg begins to break down and more water diffuses into the egg. Just before hatching, the chorion of fish eggs is slowly liquefied by proteolytic enzymes (Blaxter, 1969), and it is likely that this process occurs also in late-stage yellowfin tuna eggs . The change in buoyancy of eggs has not been studied extensively in tunas. Mayo (1973) reported a similar change in buoyancy in the eggs of seven taxa of scombrids from Florida waters, and we have observed a similar pattern in fertilized eggs of black skipjack (*Euthynnus lineatus*, first author, personal commun.). In nature, the adaptive significance of negative buoyancy in late-stage eggs is not clear, but presumably the process of sinking just before hatching would remove the late-stage eggs and newly hatched yolksac larvae from the neuston layer and reduce mortality caused by wave action, wind, and damage from ultraviolet radiation.

Egg size increased with female yellowfin tuna size. This is a common trait in many fish species, although a direct relationship is apparent in some stocks but not in others (Hempel and Blaxter, 1967; Marteinsdottir and Able, 1988; Chambers and Leggett, 1996). The relationship between egg size and female size is relatively unstudied in tunas and is probably less important, in terms of reproductive potential, than the relationship between fecundity and female age and size (Chambers, 1997).

For aquaculture purposes, the relationship of egg size to female size in our study could be used to determine the optimum size of broodstock females required to produce maximum egg sizes. For our original broodstock group, the largest females produced the largest eggs and larvae. However, larger egg size or hatching size had no relationship with hatching success in our study. Whether larger sizes at hatching confer some greater fitness for yellowfin tuna during prerecruit stages in nature is unclear, and may depend on processes of growth, feeding, and development that occur later during development. The ecological implications of the effects of size during early life stages of yellowfin tuna or other tuna species remain unknown and would require detailed investigations of spawning and early life history traits in wild tuna populations.

Acknowledgments

We thank the talented and dedicated staff of the Achotines Laboratory for their hard work to ensure the success of this project. The Overseas Fishery Cooperation Foundation of Japan provided the majority of the funding for the expansion of the seawater and tank systems, and they were also our collaborative partners in the development of the yellowfin tuna spawning project. S. Masuma (Fisheries Research Agency of Japan), C. Farwell and D. Thomasberg (Monterey Bay Aquarium), and H. Yoneshima (Kinki University) provided technical advice on the culture of tunas in captivity. In Panama, R. Martans, A. Franco, E. Diaz, and A. Cano (Direccion General de Recursos Marinos y Costeros) provided administrative support. R. Jope and K. Bentler (formerly of the IATTC) assisted with project logistics and purchasing. C. Montez (IATTC) skillfully prepared the figures. P. Tomlinson (IATTC) provided invaluable advice on growth curve fitting and bootstrap procedures. W. Bayliff provided helpful review comments. We wish to thank A. Suda for his assistance in the early development of the project. We would also like to thank the former and present Directors of the IATTC, J. Joseph and R. Allen, and the Chief Scientist of the Tuna-Billfish program, R. Deriso, for their support of this study.

Literature cited

Ambrose, D. A.
1996. Scombridae: mackerels and tunas. *In* Guide to the early stages of fishes in the California Current region (H. G. Moser, ed.), p. 1270–1285. Calif. Coop. Ocean. Fish. Inves., CALCOFI Atlas No. 33.

Bailey, K. M., and E. D. Houde.
1989. Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Biol. 25:1–83.

Blaxter, J. H. S.
1969. Development: eggs and larvae. *In* Fish physiology (S. Hoar, and D. J. Randall, eds.), p. 177–252. Academic Press Inc., New York, NY.

Boehlert, G. W., and B. C. Mundy.
1994. Vertical and onshore-offshore distributional patterns of tuna larvae in relation to physical habitat features. Mar. Ecol. Prog. Ser. 107:1–13.

Bye, V. J.
1984. The role of environmental factors in the timing of reproductive cycles. *In* Fish reproduction: strategies and tactics (G. W. Potts, and R. J. Wootton, eds.), p. 187–205. Academic Press Inc., London, UK.

Chambers, R. C.
1997. Environmental influences on egg and propagule sizes in marine fishes. *In* Early life history and recruitment in fish populations (R. C. Chambers, and E. A. Trippel, eds.), p. 63–102. Chapman and Hall, London, UK.

Chambers, R. C., and W. C. Leggett.
1996. Maternal influences on variation in egg sizes in temperate marine fishes. Am. Zool. 36:180–196.

Chow, S., V. P. Scholey, A. Nakazawa, D. Margulies, J. B. Wexler, R. J. Olson, and K. Hazama.
2001. Direct evidence for Mendelian inheritance of the variations in the ribosomal protein gene introns in yellowfin tuna (*Thunnus albacares*). Mar. Biotechnol. 3: 22–26.

Collette, B. B., and C. E. Nauen.
1983. FAO species catalogue, vol. 2, Scombrids of the

world: An annotated and illustrated catalogue of tunas, mackerels, bonitos and related species known to date. FAO Fish. Synop. 125, vol. 2, 137 p.

Davis, T. L. O., V. Lyne, and G. P. Jenkins.
1991. Advection, dispersion and mortality of a patch of southern bluefin tuna larvae *Thunnus maccoyii* in the East Indian Ocean. Mar. Ecol. Prog. Ser. 73:33–45

Farley, J. H., and T. L. O. Davis.
1998. Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*. Fish. Bull. 96:223–236.

Fritzsche, R. A.
1978. Development of fishes of the Mid-Atlantic Bight: An atlas of egg, larval, and juvenile stages, V, Chaetodontidae through Ophidiidae. U.S. Dep. Interior, Fish Wildl. Serv., Biol. Serv. Prog. FWS/OBS-78/12, 340 p.

Goetz, F. W.
1983. Hormonal control of oocyte final maturation and ovulation in fishes. *In* Fish physiology, vol. 9B, Reproduction: behavior and fertility control (W. S. Hoar, D. J. Randall, and E. M. Donaldson, eds.), p. 117–170. Academic Press, Inc., New York, NY.

Goldberg, S. R., and D. W. K. Au.
1986. The spawning of skipjack tuna from southeastern Brazil as determined from histological examination of ovaries. *In* Proceedings of the ICCAT conference on the International Skipjack Year Program (P. E. K. Symons, P. M. Miyake, and G. T. Sakagawa, eds.), p. 277–284. International Commission for the Conservation of Atlantic Tunas, Madrid, Spain.

Hempel, G., and J. H. S. Blaxter.
1967. Egg weight in Atlantic herring (*Clupea harengus* L.). J. Cons., Cons. Int. Explor. Mer 31:170–195.

Hunter, J. R., B. J. Macewicz, and J. R. Sibert.
1986. The spawning frequency of skipjack tuna, *Katsuwonus pelamis*, from the South Pacific. Fish. Bull. 84:895–903.

Johannes, R. E.
1978. Reproductive strategies of coastal marine fishes in the tropics. Environ. Biol. Fish. 3:65–84.

Joseph, J.
1963. The fecundity of yellowfin tuna (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) from the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 7:255–292.

Kaji, T., M. Tanaka, M. Oka, H. Takeuchi, S. Ohsumi, K. Teruya, and J. Hirokawa.
1999. Growth and morphological development of laboratory-reared yellowfin tuna *Thunnus albacares* larvae and early juveniles, with special emphasis on the digestive system. Fish. Sci. 65:700–707.

Kaji, T., M. Tanaka, Y. Takahashi, M. Oka, and N. Ishibashi.
1996. Preliminary observations on development of Pacific bluefin tuna *Thunnus thynnus* (Scombridae) larvae reared in the laboratory, with special reference to the digestive system. Mar. Freshw. Res. 47:261–269.

Lam, T. J.
1983. Environmental influences on gonadal activity in fish. *In* Fish physiology, vol. 9B, Reproduction: behavior and fertility control (W. S. Hoar, D. J. Randall, and E. M. Donaldson, eds.), p. 65–116. Academic Press, Inc., New York, NY.

Lauth, R. R., and R. J. Olson.
1996. Distribution and abundance of larval Scombridae in relation to the physical environment in the northwestern Panama Bight. Inter-Am. Trop. Tuna Comm., Bull. 21:127–167.

Leis, J. M., T. Trnski, M. Harmelin-Vivien, J.-P. Renon, V. Dufour, M. K. El Moudni, and R. Galzin.
1991. High concentrations of tuna larvae (Pisces: Scombridae) in near-reef waters of French Polynesia (Society and Tuamotu Islands). Bull. Mar. Sci. 48:150–158.

Liley, N. R., K. H. Olsen, and C. J. Foote.
1991. Reproductive pheromones in rainbow trout, *Oncorhynchus mykiss*, and kokanee salmon, *O. nerka*. *In* Proceedings of the fourth international symposium on the reproductive physiology of fish (A. P. Scott, J. P. Sumpter, D. E. Kime, and M. S. Rolfe, eds.), p. 188–193. FishSymp 91, Dept. Animal Plant Sci., The University of Sheffield, Sheffield, UK.

Margulies, D.
1993. Assessment of the nutritional condition of larval and early juvenile tuna and Spanish mackerel (Pisces: Scombridae) in the Panama Bight. Mar. Biol. 115: 317–330.

Margulies, D., J. B. Wexler, K. T. Bentler, J. M. Suter, S. Masuma, N. Tezuka, K. Teruya, M. Oka, M. Kanematsu, and H. Nikaido.
2001. Food selection of yellowfin tuna, *Thunnus albacares*, larvae reared in the laboratory. Inter-Am. Trop. Tuna Comm., Bull. 22: 9–51.

Marteinsdottir, G., and K. W. Able.
1988. Influence of egg size on embryos and larvae of *Fundulus heteroclitus* (L.). J. Fish. Biol. 41:883–896.

Mayo, C. A.
1973. Rearing, growth, and development of the eggs and larvae of seven scombrid fishes from the Straits of Florida. Ph.D. diss., 127 p. Univ. Miami, Miami, FL.

McPherson, G. R.
1991. Reproductive biology of yellowfin tuna in the eastern Australian fishing zone, with special reference to the north-western Coral Sea. Aust. J. Mar. Freshw. Res. 42: 465–477.

Miyashita, S., O. Murata, Y. Sawada, T. Okada, Y. Kubo, Y. Ishitani, M. Seoka, and H. Kumai.
2000a. Maturation and spawning of cultured bluefin tuna, *Thunnus thynnus*. Suisanzoshoku 48:475–488.

Miyashita, S., Y. Sawada, T. Okada, O. Murata, and H. Kumai.
2001. Morphological development and growth of laboratory-reared larval and juvenile *Thunnus thynnus* (Pisces: Scombridae). Fish. Bull. 99:601–616.

Miyashita, S., Y. Tanaka, Y. Sawada, O. Murata, N. Hattori, K. Takii, Y. Mukai, and H. Kumai.
2000b. Embryonic development and effects of water temperature on hatching of the bluefin tuna, *Thunnus thynnus*. Suisanzoshoku 48:199–207.

Nikaido, H., N. Miyabe, and S. Ueyanagi.
1991. Spawning time and frequency of bigeye tuna, *Thunnus obesus*. Nat. Res. Inst. Far Seas Fish., Bull. 28:47–73.

Nishikawa, Y., M. Honma, S. Ueyanagi, and S. Kikawa.
1985. Average distribution of larvae of oceanic species of scombroid fishes, 1956–1981. Far Seas Fish. Res. Lab., S. Ser. 12, 99 p.

Nishikawa, Y., and D. W. Rimmer.
1987. Identification of larval tunas, billfishes and other scombroid fishes (suborder Scombroidei): an illustrated guide, 20 p. CSIRO Mar. Lab. Rep. 186.

Niwa, Y., A. Nakazawa, D. Margulies, V. P. Scholey, J. B. Wexler, and S. Chow.
2003. Genetic monitoring for spawning ecology of captive yellowfin tuna (*Thunnus albacares*) using mitochondrial DNA variation. Aquaculture 218:387–395.

Ramon, D., and K. Bailey.
1996. Spawning seasonality of albacore, *Thunnus alalunga*, in the south Pacific Ocean. Fish. Bull. 94: 725–733.

Richards, W. J.
2006. Scombridae: mackerels and tunas. *In* Early stages of Atlantic fishes, vol. 2, An identification guide for the western central north Atlantic (W. J. Richards, ed.), p. 2187–2227. CRC Press, Taylor and Francis Group, Boca Raton, FL.

Richards, W. J., and D. C. Simmons.
1971. Distribution of tuna larvae (Pisces, Scombridae) in the northwestern Gulf of Guinea and off Sierra Leone. Fish. Bull. 69:555–568.

Schaefer, K. M.
1996. Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean. Fish. Bull. 94:98–112.
1998. Reproductive biology of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean. Inter-Am. Trop. Tuna Comm., Bull. 21:201–272.
2001a. Reproductive biology of tunas. *In* Fish physiology, vol. 19, Tuna: physiology, ecology, and evolution (B. A. Block, and E.D. Stevens, eds.), p, 225–270. Academic Press, San Diego, CA.
2001b. Assessment of skipjack tuna (*Katsuwonus pelamis*) spawning activity in the eastern Pacific Ocean. Fish. Bull. 99:343–350.

Scholey, V. P., D. Margulies, R. Olson, J. Wexler, J. Suter, and S. Hunt.
2001. Lab culture and reproduction of yellowfin tuna in Panama. Global Aqua. Advoc. 4(2):17–18.

Stacey, N. E.
1984. Control of the timing of ovulation by exogenous and endogenous factors. *In* Fish reproduction: strategies and tactics (G. W. Potts, and R. J. Wootton, eds.), p. 207–222. Academic Press Inc., London, UK.
1991. Hormonal pheromones in fish: status and prospects. *In* Proceedings of the fourth international symposium on the reproductive physiology of fish (A. P. Scott, J. P. Sumpter, D. E. Kime, and M. S. Rolfe, eds.), p. 177–181. FishSymp 91, Dept. Animal Plant Sci., The University of Sheffield, Sheffield, UK.

Suzuki, Z.
1994. A review of the biology and fisheries for yellowfin tuna, *Thunnus albacares*, in the western and central Pacific Ocean. FAO Fish. Tech. Pap. 336 (2):108–137.

Tanaka, M., T. Kaji, Y. Nakamura, and Y. Takahashi.
1996. Developmental strategy of scombrid larvae: high growth potential related to food habits and precocious digestive system development. *In* Survival strategies in early life stages of marine resources (Y. Watanabe, Y. Yamashita, and Y. Oozeki, eds.), p. 125–139. A. A. Balkema, Rotterdam, The Netherlands.

Van der Kraak, G., J. P. Chang, and D. M. Janz.
1998. Reproduction. *In* The Physiology of fishes (D. H. Evans, ed.), p. 465–488. CRC Press LLC, Boca Raton, FL.

Vetter, R. D., A. Kurtzman, and T. Mori.
1999. Diel cycles of DNA damage and repair in eggs and larvae of northern anchovy, *Engraulis mordax*, exposed to solar ultraviolet radiation. Photochem. Photobiol. 69:27–33.

Wexler, J. B., S. Chow, T. Wakabayashi, K. Nohara, and D. Margulies.
2007. Temporal variation of *in situ* growth of yellowfin tuna (*Thunnus albacares*) larvae in the Panama Bight, 1990–97. Fish. Bull. 105:1–18.

Wexler, J. B., D. Margulies, S. Masuma, N. Tezuka, K. Teruya, M. Oka, M. Kanematsu, and H. Nikaido.
2001. Age validation and growth of yellowfin tuna, *Thunnus albacares*, larvae reared in the laboratory. Inter-Am. Trop. Tuna Comm., Bull. 22:52–91.

Wexler, J. B., V. P. Scholey, R. J. Olson, D. Margulies, A. Nakazawa, and J. M. Suter.
2003. Tank culture of yellowfin tuna, *Thunnus albacares*: developing a spawning population for research purposes. Aquaculture 220:327–353.

Wild, A.
1986. Growth of yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean based on otolith increments. Inter-Am. Trop. Tuna Comm., Bull. 18: 423–482.
1994. A review of the biology and fisheries for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean. FAO Fish. Tech. Pap. 336 (2):52–107.

Wootton, R. J.
1979. Energy costs of egg production and environmental determinants of fecundity in teleost fishes. Symp. Zool. Soc. Lond. 44:133–159.

Zar, H. H.
1984. Biostatistical analysis, 2nd ed., 718 p. Prentice-Hall, Inc., Englewood Cliffs, NJ.

Re-estimation of small-scale fishery catches for U.S. flag-associated island areas in the western Pacific: the last 50 years

Dirk Zeller (contact author)[1]
Shawn Booth[1]
Gerald Davis[2]
Daniel Pauly[1]

Email address (for D. Zeller): d.zeller@fisheries.ubc.ca

[1] Fisheries Centre
2202 Main Mall
University of British Columbia
Vancouver, V6T 1Z4, Canada

[2] National Oceanic and Atmospheric Admninistration
National Marine Fisheries Service
1601 Kapiolani Blvd.
Honolulu, Hawaii 96814-4700

Abstract—Nearshore fisheries in the tropical Pacific play an important role, both culturally and as a reliable source of food security, but often remain under-reported in statistics, leading to undervaluation of their importance to communities. We re-estimated nonpelagic catches for Guam and the Commonwealth of the Northern Mariana Islands (CNMI), and summarize previous work for American Samoa for 1950–2002. For all islands combined, catches declined by 77%, contrasting with increasing trends indicated by reported data. For individual island entities, re-estimation suggested declines of 86%, 54%, and 79% for Guam, CNMI, and American Samoa, respectively. Except for Guam, reported data primarily represented commercial catches, and hence under-represented contributions by subsistence and recreational fisheries. Guam's consistent use of creel surveys for data collection resulted in the most reliable reported catches for any of the islands considered. Our re-estimation makes the scale of under-reporting of total catches evident, and provides valuable baselines of likely historic patterns in fisheries catches.

Manuscript submitted 26 June 2006 to the Scientific Editor.

Manuscript approved for publication 17 October 2006 by the Scientific Editor.

Fish. Bull. 105:266–277 (2007).

Small-scale nearshore fisheries in the tropical Pacific are of fundamental importance for subsistence, social and cultural purposes, in addition to providing food, trade, and recreational resources (e.g., Dalzell et al., 1996). These fisheries commonly play a vital role in providing a secure supply of protein on many Pacific Islands. Yet, catches for the small-scale fisheries in these islands are typically not estimated by the fisheries agencies. This lack of data on estimated catch applies especially to the non-commercial sectors (e.g., subsistence and recreational) and is generally justified by real or perceived difficulties and costs associated with quantification of these very spatially dispersed fisheries. Hence, extractions of these marine resources are usually underestimated in official statistics, as are their economic and social importance (Zeller et al., 2006b).

An approach to retroactively estimate catches in cases where reliable time series data are lacking applies a "re-estimation" approach to approximate historic catch time series (Zeller et al., 2006a). Such an approach typically requires subjective inferences and interpolations. This approach is justified, despite data uncertainties, given the less acceptable alternative outcome, namely that subsequent users of the available data will interpret nonreported or missing data as zero catches.

Without accounting for total catches from all sectors, it is not possible to obtain any comprehensive measure of the formal and informal economic value of these resources, or of the risks excessive fishing may represent to an island entity. The lack of these two measures is of concern, given that human population growth rates in many Pacific island countries are high and natural resources in these islands are limited. Furthermore, the growing shift from predominantly subsistence to market-based cash-oriented economies, as well as increasing development since World War II, has contributed to declines in coastal marine resources. Although localized overfishing may be responsible for some of these observed declines, anthropogenic factors such as coastal development, pollution, and poor watershed management have likely also contributed to the degradation and reduction of coastal habitat and in the productivity of the resource (Friedlander and DeMartini, 2002).

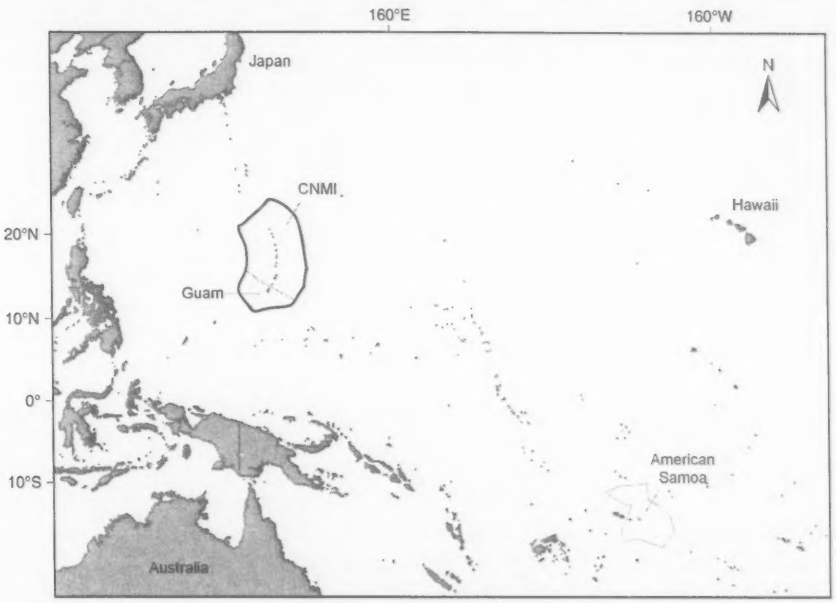


Figure 1

Location and Exclusive Economic Zones (areas outlined) of the major U.S. flag-associated island areas in the western Pacific covered in this study: Guam, Commonwealth of the Northern Mariana Islands (CNMI), and American Samoa. The Pacific Remote Island Areas (minor islands) also under U.S. flag jurisdiction are excluded from present consideration (Zeller et al.[3]). Map courtesy of A. Kitchingman and C. H. Close, *Sea Around Us* Project, Fisheries Centre, University of British Columbia.

This is particularly true close to human population centers on main islands, whereas the status of stocks in more remote areas is generally better. Obviously, places that have not experienced widespread development may still suffer stock declines because overfishing alone can deplete fishery resources on coral reefs.

The U.S. National Oceanic and Atmospheric Administration National Marine Fisheries Service (NOAA-NMFS), through its Western Pacific Fishery Information Network (WPacFIN[1]), provides data collection, assimilation, and technical reporting support to U.S. flag-associated island areas in the Pacific (Fig. 1). The coverage of this electronic information source only dates back to the early 1980s and differs between islands. There is near-complete coverage for some areas, such as Guam, and very limited coverage for others, such as Commonwealth of the Northern Mariana Islands (CNMI). For the U.S. western Pacific region, this centralized data depository is largely the result of the development of WPacFIN programs in each of the island areas in the early 1980s. All the islands considered here have few legislative requirements for reporting of catches; however, some, such as American Samoa, have instituted legal mandates that require the number of fish sold be reported. Generally, the focus of reported data has been primarily on commercial harvests (e.g., the small-boat based fisheries of American Samoa) and have not covered other sectors, such as the shore-based fisheries (Zeller et al., 2006a).

However, many small-scale studies have been undertaken to assess these missing sectors, reporting local catches or catch rates for specific periods, locations, or gear types (e.g., Craig et al., 1997). Such data sources can form the foundation for deriving catches, catch rates per unit of area, or per capita catch rates during a given time interval for these sectors of the fishery. These time-point estimates provide anchor points of concrete data upon which total catch estimates can be based. Once all such data have been extracted from their disparate sources, interpolations can be employed to fill in the periods for which quantitative data are missing. Thus, the key aspect of the approach used here is psychological, and managers have to overcome the notion that no information is available, which is not only an incorrect assumption when dealing with fisheries but a profoundly misleading one

[1] Western Pacific Fishery Information Network (WPacFIN). NOAA-National Marine Fisheries Service, Pacific Islands Fisheries Science Center, 2570 Dole Street, Honolulu, 96822–2396. Website: http://www.pifsc.noaa.gov/wpacfin (accessed 1 November 2005).

(Pauly[2]). Here, we report on work undertaken for the U.S. Western Pacific Regional Fishery Management Council to account for unreported catches (Zeller et al.[3]).

Island areas

Guam Guam (13°28′N, 144°45′E) is the southernmost island in the Mariana Archipelago (Fig. 1), and has a potential coral reef ecosystem habitat area to 100 fathom (183 m) depth, within an Exclusive Economic Zone (EEZ), of approximately 276 km^2 (including offshore banks). Of this area, 202.8 km^2 are associated with the island of Guam directly (Rohmann et al., 2005). Guam's coral reef fisheries are both economically and culturally important and have been historically significant in the diet of the human population (Hensley and Sherwood, 1993). Limitations were placed on the indigenous population with regards to any large-scale fisheries development during the Japanese occupation period (Smith[4]). These limitations, together with the destruction of the Japanese fishing infrastructure at the end of WWII, resulted in a heavy reliance on subsistence fisheries in Guam into the late 1940s. The near-shore coral reefs around Guam are considered heavily fished and degraded, and concerns about overfishing were raised as early as 1970 (Hensley and Sherwood, 1993). Most of the less accessible offshore banks, however, appear to be in better condition.

Guam's domestic fisheries can be divided into two sectors (ignoring tuna transshipment and distant water fleet catches of large pelagics): small boat-based fisheries (Myers, 1993) and shore-based fisheries (Hensley and Sherwood, 1993). Because there are few full-time commercial fishermen, there is little distinction between commercial, subsistence, and recreational fishing, and many fishing trips contribute to all three segments. In the past, tidal fish-weirs were used in Guam, although their numbers declined over the decades, and the use of weirs ceased in 1989.

Catch data for both fisheries sectors have been estimated by the Guam Division of Aquatic and Wildlife Resources (DAWR) since the mid-1960s through the use of two separate creel surveys: a marina-based boat-centered creel survey (offshore survey), and a shore-based creel survey (inshore survey). The reporting of fish weir catches was mandated as part of weir-operating permits but the data were likely incomplete. Various expansion methods have been applied in the past to raise the creel survey data to island-wide catch estimates, but these have been standardized since the mid-1980s in collaboration with WPacFIN. However, specifics of the method and thoroughness of a survey, of data handling, and of analyses have varied during the earlier periods. Since the early 1980s, these survey data have been reported through WPacFIN, and are the most comprehensive series of catch estimates used in the present study.

Commonwealth of the Northern Mariana Islands (CNMI) The Commonwealth of the Northern Mariana Islands (CNMI, Fig. 1) consists of a 680 km chain of 14 volcanic islands, extending northward from Rota (14°9′N, 145°12′E) to Farallon De Pajaros (20°32′N, 144°54′E). Over 99% of the human population (69,000 in 2000) is concentrated on the three southern main islands of Saipan, Tinian, and Rota. The population has increased rapidly since the 1980s, driven by fewer restrictions on immigration and by the prosperity from the main industries—tourism and garment manufacturing.

CNMI are a group of islands with fringing reefs (surrounding most islands) and offshore coral reef banks and ridges. The conditions of local reefs vary; heavy fishing pressure is considered a problem for the sustainability of the reefs on the main islands, particularly the island of Saipan, because of its large population and more extensive coastal development.

Following WWII and the expulsion of the active Japanese fisheries, subsistence fisheries again dominated the catch. Because of the loss of most Japanese fishing vessels, and decades of Japanese restrictions on indigenous fishing outside local reefs, early subsistence catches were focused on near-shore and lagoon-based resources. Subsistence fishing for near-shore resources was an important daily activity for the local population well into the 1970s, whereas commercial and recreational fleet developments did not start until the 1960s, and westernized economic development did not accelerate until the 1970s and 1980s. The local economic boom starting in the late 1980s, driven by tourism and garment manufacturing, did not result in significant growth of the commercial fisheries sector. Thus, the local fishing industry supplied only a small part of the total seafood demand in the 1990s, and imports accounted for a growing part of the supply. Growth in recreational fisheries came instead with increased westernization of the economy which, combined with increased availability of boats, blurred the boundaries between subsistence and recreational fishing. Thus, each fishing trip today may have commercial and subsistence, as well as recreational aspects.

The Division of Fish and Wildlife (DFW) for CNMI conducted a data collection system for commercial catches since the mid-1970s but reported data have only been available since the early 1980s through WPacFIN. The estimated commercial landings in Saipan are based on a voluntary dealer purchase receipt collection system and are adjusted by WPacFIN for the remainder of CNMI. The noncommercial sector (subsistence and

[2] Pauly, D. 1998. Rationale for reconstructing catch time series. EC Fisheries Cooperation Bulletin 11:4–10.

[3] Zeller, D., S. Booth, and D. Pauly. 2005. Reconstruction of coral reef- and bottom-fisheries catches for U.S. flag island areas in the Western Pacific, 1950 to 2002. Western Pacific Regional Fishery Management Council, 1164 Bishop St., Suite 1400, Honolulu, HI 96813. Website: http://www.wpcouncil.org/bottomfish.htm (accessed 17 October 2006).

[4] Smith, R. O. 1947. Survey of the fisheries of the former Japanese mandated islands. Fishery Leaflet 273, U.S. Fish and Wildlife Service, Department of the Interior, 1849 C Street, NW, Washington, DC 20240, 105 p.

recreational fishing) has been subject to limited monitoring since 1984 and day-time creel surveys have been undertaken for the Saipan lagoon only. However, these data have not been analyzed or expanded for estimation of CNMI-wide noncommercial catches and were not available to us.

American Samoa American Samoa is the only U.S. territory south of the equator (14°20'S, 170°W, Fig. 1), and its small-scale fisheries consist of shore-based and boat-based sectors (Zeller et al., 2006a). A clear separation between commercial and noncommercial aspects in each fishery is difficult because fish from either sector can be sold or retained for personal consumption (Craig et al., 1993). The existing catch data on the predominantly commercial boat-based sector by the American Samoa Department of Marine and Wildlife Resources (DMWR) has been reported through WPacFIN since the early 1980s. The noncommercial sector, especially as relating to shore-based fisheries, is not monitored and catches are not reported on a regular basis. However, a short-lived DMWR survey of shore-based fisheries, as well as other local studies, was conducted sporadically on this sector between 1980 and 2002. Recently, total nonpelagic fisheries catches for both sectors were re-estimated back to 1950 by Zeller et al. (2006a), and these findings will be relied upon in the present study.

Aims

The purpose of our study was to assemble available information and data on catches of the small-scale, near-shore fisheries for nonpelagic species of the major U.S. flag-associated island areas in the western Pacific for 1950–2002, namely Guam, the Commonwealth of the Northern Mariana Islands (CNMI), and, in summary form, for the previously estimated catches for American Samoa (Zeller et al., 2006a). Although American Samoa's catches were published separately (Zeller et al., 2006a), they are summarized in the present study for completeness. The U.S. State of Hawaii was excluded from present considerations because the economic, social and noncommercial fishery conditions and data differed substantially from those of the other islands, and required a different method for reconstructing the data. Also excluded was the information available for the limited (predominantly recreational) catches taken on the Pacific Remote Island Areas (PRIAs or minor islands) reported on elsewhere (Zeller et al.[3]). The aim was to derive estimates of likely total removal of marine resources for the 1950–2002 period. The present re-estimation excludes pelagic species (i.e., tunas and billfishes) that are the target of large-scale fisheries, even if these species are also caught by small-scale, local sectors. Small-scale fisheries in our study targeted both deeper water species (such as lutjanids, lethrinids, and serranids), as well as coastal, reef-associated small pelagic species (such as carangids, including the culturally important big-eye scad [*Selar crumenophthalmus*]).

Materials and methods

The catch re-estimation approach utilized here consists of six general steps based on work done for the Western Pacific Regional Fishery Management Council (Zeller et al.[3]) and Zeller et al. (2006a):

1 Identification of existing reported catch times series, e.g., local reports, and data presented by the Western Pacific Fishery Information Network (WPacFIN[1]) on behalf of local agencies;
2 Identification of sectors, time periods, species, gears, etc. not covered by (1), i.e., missing catch data, via literature searches and consultations;
3 Search for available alternative information sources to supply the missing catch data in (2), through extensive literature searches and consultations with local experts;
4 Development of data anchor points in time for missing data items, and their expansion to island- or country-wide catch estimates;
5 Interpolation for time periods between data anchor points for total catch, generally with per capita catch rates; and
6 Estimation of final total catch times series estimates for total catch, combining reported catches (1) and interpolated, island-expanded missing data series (5).

Island areas differed in terms of fisheries sectors, their coverage of reported data, and available alternative information. Details of available alternative information sources for each island area, all reference material for data sources used (non-refereed publications), and the specifics of data anchor point estimation can be found in a report to the U.S. Western Pacific Regional Fishery Management Council (Zeller et al.[3]).

Guam

Catches for both boat- and shore-based fisheries sectors have been estimated by DAWR since the mid-1960s through the use of two creel surveys (offshore survey and inshore survey). In the more recent years, DAWR applied expansion methods to extrapolate island-wide catch estimates from creel survey data. The fish weir catch estimates were likely incomplete.

Because domestic fisheries in Guam are generally part commercial, part subsistence, and part recreational, the re-estimation approach taken was not by differentiation of the commercial and noncommercial sectors, but rather by following the creel-survey distinction between boat-based (offshore survey) and shore-based (inshore survey) estimations of catches (Table 1). Given our focus on nonpelagic fisheries, we excluded the trolling section for large pelagic species from the offshore catch reports and retained bottom-fishing and boat-based spear-fishing catches. Comparisons of supply and demand, with the use of reported catch (including pelagic taxa), as well as estimates of imported

seafood and domestic seafood consumption rates, were undertaken to estimate potentially unreported catches, as well as to estimate total likely catch for the 1950–64 period for which no other reported information was available (see "Supply versus demand" heading below, Table 2).

Offshore boat-based catches

1965–82: The offshore catch estimates for this time period, which pre-dates WPacFIN reporting, were drawn from the creel survey data as reported in DAWR annual reports. Procedures for expanding survey data to island-wide catches, as listed or applied by the various data sources, were generally accepted. For example, reports from earlier years indicated under-reporting due to sampling design limitations of the creel surveys by a minimum factor of two, and we adjusted the reported catch estimates correspondingly for these years (Zeller et al.[3]).

1983–2002: We relied on the island-wide expanded catch estimates as provided by WPacFIN, based on offshore creel surveys undertaken by DAWR. These data

Table 1

Data sources, available time series data, and data anchor points for catch re-estimation for Guam. DAWR: Division of Aquatic and Wildlife Resources; WPacFIN: Western Pacific Fishery Information Network. X=yes.

Sector	Year(s)	Source	Official data (reported)	Missing data (unreported)	Catch (t)
Offshore, boat-based	1965–82	Guam DAWR offshore creel survey reports	X		1–36
Offshore, boat-based	1983–2002	WPacFIN, DAWR	X		43–65
Inshore, shore-based	1965–81	Guam DAWR inshore creel survey reports	X		145–102
Inshore, shore-based	1982–84	Hensley and Sherwood (1993)		X	92–141
Inshore, shore-based	1985–2002	WPacFIN, DAWR	X		179–63
Offshore and inshore	1950	Reported consumption rate[1]		X	957

[1] Adjusted for imports and consumption of pelagic species.

Table 2

Data sources and data anchor points for import and consumption estimation, forming part of the supply (reported catch and estimated imports) and demand (consumption estimates) approach used for catch re-estimation for Guam.

Supply or demand	Item	Year(s)	Source	Comments	Annual per capita rate (kg)	Guam total (kg)
Supply	Import	1950	Assumption	Half of adjusted 1980 rate[1]	10.6	636,850
Supply	Import	1980	Import rate	17.7 kg/person/year, adjusted for cooler-shipped fish by 20%	21.2	2,250,204
Supply	Import	1999	Dept. of Commerce		19.5	2,962,380
Supply	Import	2000	Dept. of Commerce		20.5	3,180,014
Supply	Import	2002	Dept. of Commerce		20.9	3,359,137
Demand	Consumption	1950	Assumption	Same as 1980, adjusted for pelagics	26.6	1,593,940
Demand	Consumption	1980	Consumption rate	Adjusted for pelagics	26.1	2,766,977
Demand	Consumption	1985–2002	Assumption	Consumption = imports + reported catches	22.6–21.7	2,595,204–3,488,267

[1] This accounts for the lower air-and boat-based travel between islands in 1950 compared to 1980.

were reported by taxon, and thus allowed us to exclude large pelagic species.

Inshore, shore-based catches

1965–81: The inshore catch data for this period were based on the inshore creel survey data as reported in the DAWR annual reports, including the often separately reported estimates for octopus and shellfish (based on reef-gleaning), fish weirs, and the highly irregular, seasonal catches of juvenile rabbitfishes (Siganidae) and big-eye scad. Procedures for expanding the catches were accepted as reported at the time. We applied or accepted adjustment factors for nonsurveyed periods as provided or used by the fishery data sources (Zeller et al[3]). The years 1980 and 1981 were deemed poorly reported because of limited survey coverage. Therefore, we replaced the reported catches for 1980 and 1981 with the average catches for 1978–79 and 1982–83, respectively.

1982–84: Data from Hensley and Sherwood (1993) were used for the 1982–84 period because WPacFIN has reported inshore catches only since 1985. It should be noted that these data did not include those from night fisheries and therefore under-represented actual catches.

1985–2002: We used the island-wide expanded catch estimates from the inshore creel survey, as undertaken by DAWR, and provided by WPacFIN.

Supply (imports and catches) versus demand (consumption) To assess whether the reported catches as outlined above accounted for the likely total catches and to derive estimates of likely catches for the undocumented 1950–64 period, we compared estimates of total supply (reported catches plus estimated imported catches) with demand as approximated by consumption estimates. For the purpose of supply and demand estimation, we included catches of pelagic species as provided by WPacFIN and DAWR, with a fixed amount of 39 t/year carried back from 1959 to 1950, based on DAWR's estimated annual pelagic catch for 1960–62.

Imports Information on reported imports was available for 1999 and 2002 (Guam Department of Commerce[5]), which were converted to per capita rates (1999: 19.5 kg/person; 2002: 20.9 kg/person) using human population statistics (U.S. Census Bureau[6]), and for 1980 as an estimated annual per capita import rate of 17.7 kg (Table 2). There is a long-standing tradition of bringing fish into Guam as part of personal travel. A large, but unknown portion of these imports are so-called cooler-shipped fish and are primarily from the Federated States of Micronesia, Palau, and the Republic of the Marshall Islands. These imports have been poorly recorded, especially in the earlier periods. To account for under-reporting of cooler-shipped imports in earlier years, we adjusted the 1980 annual per capita import rate by 20%, to 21.2 kg. For 1950, we assumed a level of import of half of the adjusted 1980 import rate (i.e., 10.6 kg; Table 2), to account for the much lower air- and boat-based travel between the various islands in 1950 compared to 1980. We linearly interpolated import rates between the 1950, 1980, 1999, and 2002 import data anchor point estimates and expanded these to total import estimates using human population statistics.

Another factor that may have influenced rates of import and harvest is aquaculture. There is potentially a considerable (but unknown) volume of locally farmed tilapia, catfish, and milkfish that is sold without regulation through small-scale markets and road-side vendors, and these products are not reported or recorded. Currently, it is not possible to estimate the impact of aquaculture on the present estimation of catches.

Demand Estimates of demand were based on the reported annual per capita consumption rate of 27 kg of seafood for 1980 (Zeller et al[3])—a rate that was carried back unaltered to 1950. We thus assumed the same relative consumption patterns for 1950 as for 1980, which may underestimate the seafood consumption patterns for 1950, and thus is adding a conservative component to our estimation. We accounted for the consumption of pelagic species by removing the reported catches of pelagic species for each year from total consumption for that year, and subsequently derived estimated nonpelagic per capita consumption rates with population statistics (Table 2).

For 1985–2002, we assumed that total consumption was accounted for by the sum of reported catches plus estimated imported catches. Total consumption was adjusted by removing the reported pelagic catches, and the 1985–2002 per capita nonpelagic consumption rates were derived with human population statistics (Table 2).

For the 1981–84 period, we interpolated per capita nonpelagic consumption rates between the 1980 and 1985 data anchor points. The growing concern about market dumping of incidental bycatch from the pelagic transshipment fleet onto the local seafood market was not considered in the present study because it is thought to be a relatively recent phenomenon. It would be reflected in declining commercial reported catch data because it replaces local fish in the commercial market supply.

Supply versus demand To derive estimates of catches for the 1950–64 period, we assumed that domestic seafood supply was either locally caught, relying heavily on subsistence fishing, or was part of the cooler-shipped imports. Given the assumed imports, the likely total local catches were derived as the difference between import estimates and consumption estimates (Table 2). Thus, in 1950, an assumed per capita import of 10.6 kg of seafood and an estimated per capita consump-

[5] Guam Department of Commerce. 2005. Website: http://www.admin.gov.gu/commerce (accessed 15 January 2005).

[6] U.S. Census Bureau. 2005. Website: http://www.census.gov/cgi-bin/ipc/idbsprd (accessed 15 January 2005).

Table 3

Data sources, available time series data, and data anchor points for catch re-estimation for the Commonwealth of the Northern Mariana Islands. WPacFIN=Western Pacific Fishery Information Network; DFW=Division of Fish and Wildlife.

Sector	Year(s)	Source	Official data (reported)	Missing data (unreported)	Catch (t)
Commercial	1960	No commercial fishing		X	0
Commercial	1983–2002	WPacFIN, DFW	X		76–106
Noncommercial	1950	Per capita consumption		X	456[1]
Noncommercial	1984	Proportion of total catch		X	166[2]
Noncommercial	1993–2002	Proportion of total catch		X	87–106[3]

[1] Reported per capita seafood consumption of 0.45 kg/day was reduced by 50% to remain a conservative estimate.

[2] In 1984 noncommercial catches represented about 63% of total catches, corresponding to a noncommercial to commercial ratio of 1.7:1.

[3] By the early 1990s, the noncommercial catch accounted for about 50% of total catches. This ratio was carried to 2002.

tion rate of 26.6 kg, implied a per capita catch rate of 16.0 kg for 1950.

For the 1965–84 period, the difference between reported catches and supply/demand estimates was interpreted as unreported catches (e.g., unrecorded night fisheries catches in the early 1980s), and were added to the reported catches (since 1965), resulting in the final re-estimated total catches.

Catch rates We converted re-estimated catches into per capita catch rates using human population statistics and catch per unit area of the depth-defined potential coral reef ecosystem habitat area (*sensu* Rohmann et al., 2005). Given that most nonpelagic catches come from areas relatively close to Guam, we used the potential reef area estimate (to 100 fathom=183 m depth) for reefs associated directly with the island of Guam (202.8 km^2), not the reef area estimate for the EEZ (276 km^2; Rohmann et al., 2005). The reef area may slightly underestimate the area for bottom-fisheries, particularly for the post-1980 period, when an increasing proportion of commercial bottomfish catches (up to 30%) likely originated from offshore banks.

CNMI

Commercial catches Estimates based on data collected by DFW of commercial landings for recent years (1981–2002) were available through WPacFIN. Given uncertainty surrounding the low catches reported for the first few years of this data series, only the period from 1983 through 2002 was used (Table 3). Because the collected data relate to Saipan only, WPacFIN uses an adjustment factor of 20% to expand to CNMI total catches, which is thought to account for much of the known under-recording of commercial landings. Because there was little local commercial fisheries development in the CNMI until the 1960s, we assumed commercial catches were zero in 1960 (Table 3) and linearly interpolated catches between 1960 and the 1983 value as reported by WPacFIN.

Noncommercial catches Noncommercial catches are not reported in CNMI. Although limited monitoring has existed since 1984 for the Saipan lagoon only, these data have not been analyzed and were not available to us.

1950–83: Subsistence fishing was an important daily activity in the Northern Marianas after WWII, and it was estimated that in the late 1940s the local population traditionally consumed nearly 0.45 kg/person/day, implying an annual per capita seafood consumption of over 165 kg (Smith[4]). Although this rate of consumption may appear a high estimate, other Pacific islands have reported similarly high annual per capita consumption rates as recently as the late 1990s, e.g., Kiribati (183 kg), Palau (124 kg), Federated States of Micronesia (119 kg), or Tuvalu (113 kg) (Gillett[7]). To account for lower fish consumption by the small nonindigenous population, the likely inclusion of pelagic species in the reported consumption rate, and U.S. military food support after WWII, as well as to remain conservative in our estimation, we reduced this rate by over 50% to 72.6 kg/person/year (0.2 kg/person/day) as the assumed per capita consumption rate for 1950 (Table 3). Furthermore, given that virtually no vessels were available for exploitation of offshore resources shortly after WWII, we assumed that noncommercial catches in 1950 were based almost exclusively on near-shore resources. We linearly interpolated the per capita catch rates between this 1950 level and the catch rate estimated for 1984 (see below) and expanded these to a total noncommercial catch estimate with the use of human population census data.

1984–2002: In 1984, noncommercial catches were thought to have accounted for approximately 63% of total catches, which corresponded to a noncommercial-

[7] Gillett, R. 2002. Pacific Island fisheries: regional and country information. RAP Publication 2002/13, 168 p. Asia-Pacific Fishery Commission, FAO Regional Office for Asia and the Pacific, Maliwan Mansion, Phra Atit Road, Bangkok 10200, Thailand.

Table 4

American Samoa reconstructed catch summary, by decade. Summarized from Zeller et al. (2006a).

Year	Official reported catch (t)	Unreported catch (t)	Total estimated catch (t)
1950	—	752	752
1960	—	635	635
1970	—	596	596
1980	41	368	409
1990	10	312	322
2000	42	152	195
2002	34	121	155

to-commercial catch ratio of 1.7:1 (Table 3). By the early 1990s, approximately 50% of total catches were thought to be not reported because they constituted noncommercial catches. Thus, the noncommercial catch value for the time period 1993–2002 was set equal to the total commercial catches (Table 3). Thus, we assumed higher reliance on noncommercial fishing in the early 1980s compared to the 1990s. We interpolated the proportion of noncommercial catches between 1984 and 1993 and expanded them by using reported commercial catches.

Catch rates Re-estimated catches were converted to per capita catch rates by using human population census data, and to catch per unit area of the depth-defined potential coral reef ecosystem habitat area (*sensu* Rohmann et al., 2005). Total potential coral reef area to a depth of 100 fathoms (183 m) for CNMI is 476 km^2 (Rohmann et al., 2005). Given that most fishing in CNMI occurs near the three main islands, the coral reef area estimate for these islands (331.2 km^2) was used here also (Rohmann et al., 2005).

American Samoa

Total catches for nopelagic species for American Samoan have been re-estimated independently by Zeller et al. (2006a), and are summarized by decade in Table 4. American Samoan catches were included in the present study for completeness in the re-estimation of total time series catches for the U.S. flag-associated Pacific island areas.

Results

The catch re-estimation for nonpelagic species for the major U.S. flag-associated island areas in the western Pacific combined (excluding Hawaii) indicated two main points (Fig. 2A):

1 a substantial discrepancy between officially reported catch data and potential total catches as re-estimated here and by Zeller et al. (2006a). For the time period for which reported data existed (1965–2002), such data may have yielded an underestimate of likely total catches by as much as a factor of 4.55. This discrepancy was largest in early years; and
2 a potential decline of 77% occurred in total catches, from an estimated 2165 t in 1950 to 496 t in 2002. This decline contrasted with the trend observed from the data reported by individual island entities—namely an increasing trend from 147 t in 1965 to 269 t in 2002.

Individual islands

For Guam, the re-estimation indicated a decline of 86% in catches of nonpelagic species over the 50-year time period considered here. There was also a 2.5-fold difference between the re-estimated catches and the reported statistics for the 1965–2002 period, driven by underreporting of catches in earlier periods. Guam's ongoing commitment to and consistent application of creel surveys to estimate total catches has resulted in what may be the most reliable estimates of total catches for any of the islands considered here, at least since the mid-1980s (Fig. 2B). Based on the re-estimated data, the annual per capita catch rates for Guam's coral reef- and bottom-fisheries may have declined from 16.0 kg to 0.8 kg between 1950 and 2002 (Table 5). Catch rates per area of potential coral reef habitat (to 100 fathom=183 m depth) appear to have declined from 4.7 t/km^2/year to 0.6 t/km^2/year between 1950 and 2002 (Table 5).

For CNMI, the re-estimated catches indicated a decline of about 54% in catches of nonpelagic species between 1950 and 2002. Comparing the catches reported by CNMI from WPacFIN with the re-estimated total catches, we found a 2.2-fold under-reporting of potential total catches by the reported data, compared to the re-estimated totals for the 1983–2002 time period of coverage by WPacFIN (Fig. 2C). Taking into account CNMI's rapid human population growth over the last two decades, we surmise that the annual per capita catch rate may have declined from a high of 72.6 kg in

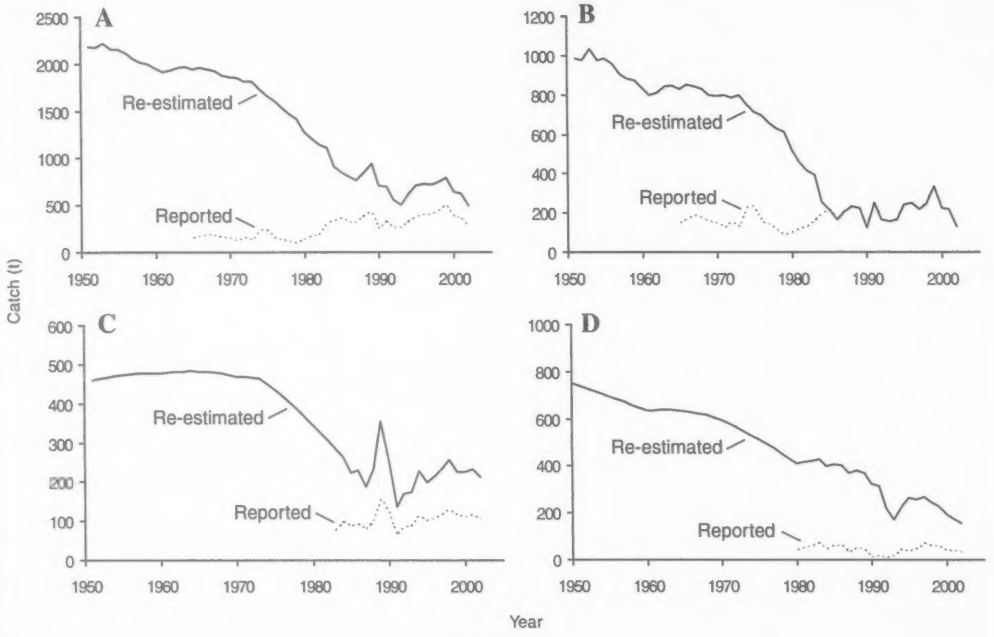


Figure 2

Re-estimated catches of small-scale, coral-reef fisheries for the major U.S. flag-associated island areas in the western Pacific (Guam, Commonwealth of the Northern Mariana Islands [CNMI], and American Samoa), versus the statistics officially reported by these island entities through the Western Pacific Fishery Information Network. Both the under-representation of likely total catches, as well as the likely decline in catches is evident in each case. Total re-estimated catches (**A**) summed over all the major U.S. flag-associated island areas of the western Pacific considered here; (**B**) for Guam versus the catches reported by Division of Aquatic and Wildlife Resources; (**C**) for CNMI versus the statistics officially reported by Division of Fish and Wildlife; and (**D**) for American Samoa versus the statistics officially reported by Department of Marine and Wildlife Resources (Figure 2D modified from Zeller et al., 2006a).

Table 5

Catch rates for the re-estimated small-scale fishery catches for Guam and the Commonwealth of the Northern Mariana Islands (CNMI), excluding pelagic species. Catch estimates are presented as per capita catch rates, and as catch per surface area of potential coral reef habitat to a depth of 100 fathom (183 m, Rohmann et al., 2005).

	Per capita catch (kg/year)		Catch/area (t/km^2/year)		
				Commonwealth of the Northern Mariana Islands	
Year	Guam	Commonwealth of the Northern Mariana Islands	Guam (202.8 km^2)	All islands (476 km^2)	Main islands (331.2 km^2)
1950	16.0	72.6	4.7	1.0	1.4
1960	12.5	53.9	4.1	1.0	1.4
1970	9.4	37.9	3.9	1.0	1.4
1980	4.9	20.5	2.5	0.7	1.0
1990	1.0	5.8	0.6	0.5	0.8
2000	1.4	3.2	1.1	0.5	0.7
2002	0.8	2.9	0.6	0.4	0.6

1950 to 2.9 kg by 2002 (Table 5). Given that over 99% of the human population of CNMI lives around the three main islands, the catch per reef habitat area was assessed for both the entire CNMI reef area (476 km^2) and also for the reef areas of the three main islands (331.2 km^2). Thus, between 1950 and 2002, estimated annual catch per km^2 reef area appears to have declined from 1.0 t to 0.4 t, and from 1.4 t to 0.6 t for the entire CNMI reef area (476 km^2) and main islands reef areas (331.2 km^2), respectively (Table 5).

The historic fisheries catches for American Samoa, as re-estimated by Zeller et al. (2006a), indicated a potential decline of about 79% in small-scale fisheries catches of nonpelagic species between 1950 and 2002 (Fig. 2D; modified from Zeller et al., 2006a). There was also a 7-fold difference between the re-estimated catches and the reported data for the 1980–2002 time period.

Discussion

Local and regional fisheries experts often acknowledge that they are aware of the limited nature of much of the official data, but rarely are willing or able to quantify the missing catches. Our re-estimation makes the potential scale of under-reporting of total extractions of marine resources evident. Specifically, our study illustrates not only the potential discrepancy by a factor of 4.55 between what was reported and what may have been caught (for the period of data reporting), but also indicates the potential scale of declines (77% overall for all areas combined) in total catches over the last 50 years. Although the historic catch estimates proposed here obviously do not represent a formal stock assessment, they are useful as baselines of potential historic patterns and trends in fisheries catches.

Regarding our comparison of catch data to those from official, reported fisheries, we acknowledge that most fisheries statistics were originally designed as an economic development and monitoring tool, where there was a common focus on commercial catches (with the exception of Guam). Nevertheless, reported data are being increasingly used to present national and global fisheries conditions and status and trends of resources. Thus, the under-representation of likely total catches as indicated here may lead directly to an erroneous interpretation of the status of fisheries within the U.S. flag-associated islands. Significantly, the situation of under-reporting contributes to the continued marginalization of small-scale fisheries (Pauly, 1997), and the ongoing under-valuation of the direct and indirect economic and social contribution of noncommercial (e.g., subsistence, and increasingly recreational) fisheries to the economic well-being of these islands (Zeller et al, 2006b). Such underestimations of catch histories may also have repercussions for the move towards ecosystem-based fisheries management.

The general approach used here, which relies on anchor points of data obtained from a variety of peer-reviewed and non-refereed data sources, moderated by conservative assumptions, and interpolated for missing-data years, results in catch estimates that accounted for all fisheries sectors. We acknowledge that our estimates clearly are not statistically rigorous in the sense of approximating "true" time-series values, which are obviously not known. However, given our conservative approach to estimation, the present estimates are less wrong than the current default of reporting zero catch for fisheries sectors not considered in official figures. Ignoring the catches of noncommercial sectors of fisheries in the U.S. flag-associated island areas of the western Pacific has likely resulted in a skewed picture of the historic catch trends, as well as the magnitude of catches for nonpelagic, near-shore resources in these islands.

Catch estimation procedures such as ours are associated with high data uncertainty; this is the nature of alternative, non-standardized data sources. The paucity of data for the earlier periods was an acknowledged shortcoming to our approach; nevertheless, our approach is based on the best data and information available. We endeavored to remain conservative in our estimation throughout the period of examination; thereby incorporating a precautionary aspect into the data. Our conservative approach can be placed into context by the following consideration.

The re-estimation of catches for Guam, as undertaken here, indicates a decline in catches of 86%, and a 2.5-fold discrepancy between the re-estimated catches and the reported statistics over the time period for which DAWR reported data exist (1965–2002). The validity of the differences between reported and re-estimated catches is supported by the observation that, at least for the earlier periods, the catch data as reported by our sources (and forming the reported data) were "probably several times" less than the actual yields (Zeller et al.[3]).

Concerns about our approach to the unreported catches can be placed into perspective through an alternative, albeit less rigorous estimation (Zeller et al.[3]). In 1977, 38.6% of households in Guam were considered to have at least one family member who fished, and mean monthly catch per surveyed household was 32.7 kg, or 392 kg/year. With an average of 5 people per household and a population of 110,000 in 1977 for Guam, these figures imply 22,000 households (110,000 people/5 people per household), of which 38.6% (i.e., 8492 households) had active fishermen. These actively fishing households alone could thus have caught 3,328,864 kg in 1977 (8492 households with catch rate of 392 kg). Accounting for pelagic fish in their catch (45.8% of reported catches in 1977 were caught with pelagic gear), this calculation would imply a nonpelagic catch of 1,804,244 kg for 1977 (3,328,864 kg×[1–0.458]). This admittedly very indirect estimate is 2.76 times our total reconstructed nonpelagic catch estimate of 654,345 kg for 1977, and 12.6 times the DAWR reported catch of 143,220 kg. Thus, this indirect approximation supports our contention that our re-estimation approach was conservative, and total catches in the earlier periods were considerably higher than those of the reported data.

We appreciate that using linear interpolation of per capita catch rates between anchor points (particularly if widely spaced in time) may introduce additional data uncertainties associated with potential behavioral (changes in lifestyle and dietary preferences) and socioeconomic (move towards cash-economy) changes in the human population over that time period. This uncertainty in turn may lead to over- or underestimation of catches for a given year, for the period between anchor points. However, given the bounds provided by the anchor point data, such uncertainties would primarily influence the shape of the resultant catch curve for the period between each set of anchor points. Given the paucity of other supportive data, the only reliable alternative approach would have been a simple linear interpolation of catches between anchor points. On closer examination of our reconstructed data (see Fig. 2, the source of present data [Zeller et al.[3]], and Zeller et al., 2006a), such linear interpolation would only result in relatively small differences compared to our present approach. For example, a simple linear interpolation of anchor point catches would have smoothed the slight rise in reconstructed catches for CNMI between 1950 and 1980 (Fig. 2C). Overall, however, the broad conclusions and general trends observed here would not have been substantially affected.

The area catch rates as estimated here indicate catch rates ranging from 0.4 to 4.7 t/km^2/year. These estimates are all at or near the lower end of the only other comprehensive range of estimates (0.3–64 t/km^2/year) established for the Pacific region (Dalzell and Adams, 1997). However, all area catch rates are heavily influenced by the definition of coral reef area, which here was taken as depth defined (100 fathoms=183 m) potential coral reef ecosystem habitat as defined by Rohmann et al. (2005), which may represent overestimates of true coral reef habitats around each island. Nevertheless, the present estimates indicate that our reconstructed catch estimates, even for the early years, may likely be feasible in a broader ecological context.

Although the overall finding of our study was that of declining total catches, such declining catches may not necessarily be the result of excessive fishing alone because other factors may also contribute to the decline. These include changes in lifestyles, cash incomes, and dietary preferences of the local populations (as indicated above), as well as habitat degradation and pollution resulting from environmentally insensitive developments (Friedlander and DeMartini, 2002). All these factors can potentially lead to declines in the size of fish stocks and catches. Nevertheless, our results do indicate likely substantial changes over the last 50+ years in fisheries catches and should form important baselines for a move towards ecosystem-based resource and habitat management in the U.S. western Pacific region, particularly as other lines of evidence (e.g., declines in mean size of fish) also indicate that overfishing or stock declines may indeed be occurring in many areas (e.g., Craig et al., 1993).

Finally, and in our opinion significantly, we suggest strongly that all responsible agencies should be required to implement and maintain regular estimation procedures to account for and report all catches taken by all fisheries sectors. According to the data from the present study, Guam may offer a good example and starting point for such considerations. Guam has established an active commitment to creel surveys during the last 20+ years as a mechanism to estimate total catches. It is to be hoped that this commitment will continue. Given the high costs of creel surveys (which are the most suitable method for estimating highly dispersed and de-centralized noncommercial fisheries), resource-limited developing countries should give considerations to regular, albeit nonannual surveys for estimation of noncommercial catches. Well executed and comprehensive noncommercial catch estimates undertaken every 2–5 years are better than the current scenario of virtually no data collection.

Management agencies and policy makers should consider the distinctly different baselines of past catches as presented in this study, as they shed new light on issues and concerns for fisheries sustainability and ecosystem conservation. Furthermore, re-estimations, as presented here, illustrate the importance of small-scale and noncommercial fisheries sectors and indicate a need to account for all fisheries catches in official statistics.

Acknowledgments

We thank the Western Pacific Regional Fishery Management Council for funding the present study. The data provided by D. Hamm from the Western Pacific Fishery Information Network (WPacFIN) at the Pacific Islands Fishery Science Centre, NMFS, NOAA, are greatly appreciated. Critical comments by R. Clarke, E. DeMartini, D. Fenner, T. Graham, D. Hamm, K. Lowe, and W. Walsh contributed significantly to this study and are greatly appreciated. The statements, findings, conclusions, and recommendations are those of the authors and do not necessarily reflect the views of NOAA, Guam DAWR, American Samoa DMWR, or CNMI DFW. D. Zeller, S. Booth and D. Pauly acknowledge the support of the Pew Charitable Trusts for funding the *Sea Around Us* project at the University of British Columbia Fisheries Centre.

Literature cited

Craig, P., B. Ponwith, F. Aitaoto, and D. Hamm.
1993. The commercial, subsistence, and recreational fisheries of American Samoa. Mar. Fish. Rev. 55: 109–116.

Craig, P., J. H. Choat, L. M. Axe, and S. Saucerman.
1997. Population biology and harvest of the coral reef surgeonfish *Acanthurus lineatus* in American Samoa. Fish. Bull. 95:680–693.

Dalzell, P., T. J. H. Adams, and N. V. C. Polunin.
1996. Coastal fisheries in the pacific islands. Oceanogr. Mar. Biol. Ann. Rev. 34:395–531.

Dalzell, P., and T. J. H. Adams.
1997. Sustainability and management of reef fisheries in the Pacific Islands. Proc. 8th Int. Coral Reef Sym. 2:2027–2032.

Friedlander, A., and E. E. DeMartini.
2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. Mar. Ecol. Prog. Ser. 230:253–264.

Hensley, R. A., and T. S. Sherwood.
1993. An overview of Guam's inshore fisheries. Mar. Fish. Rev. 55:129–138.

Myers, R. F.
1993. Guam's small-boat-based fisheries. Mar. Fish. Rev. 55:117–128.

Pauly, D.
1997. Small-scale fisheries in the tropics: marginality, marginalization, and some implications for fisheries management. *In* Global trends: fisheries management (E. K. Pikitch, D. D. Huppert, and M. P. Sissenwine, eds.), p. 40–49. Am. Fish. Soc. Symp. 20, Bethesda, MD.

Rohmann, S. O., J. J. Hayes, R. C. Newhall, M. E. Monaco, and R. W. Grigg.
2005. The area of potential shallow-water tropical and subtropical coral ecosystems in the United States. Coral Reefs 24:370–383.

Zeller, D., S. Booth, P. Craig, and D. Pauly.
2006a. Reconstruction of coral reef fisheries catches in American Samoa, 1950–2002. Coral Reefs 25:144–152.
2000b. Fisheries contributions to GDP: underestimating small-scale fisheries in the Pacific. Mar. Res. Econ. 21:355–374.

Whole-gear efficiency of a benthic survey trawl for flatfish

David A. Somerton (contact author)
Peter T. Munro
Kenneth L. Weinberg
National Marine Fisheries Service, NOAA
Alaska Fisheries Science Center
7600 Sand Point Way NE
Seattle, Washington 98115
Email address for D. A. Somerton: david.somerton@noaa.gov

Abstract—Whole-gear efficiency (the proportion of fish passing between the otter doors of a bottom trawl that are subsequently captured) was estimated from data collected during experiments to measure the herding efficiency of bridles and doors, the capture efficiency of the net, and the length of the bridles sufficiently close to the seafloor to elicit a herding response. The experiments were focused on four species of flatfish: arrowtooth flounder (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), rex sole (*Glyptocephalus zachirus*), and Dover sole (*Microstomus pacificus*). Whole-gear efficiency varied with fish length and reached maximum values between 40% and 50% for arrowtooth flounder, flathead sole, and rex sole. For Dover sole, however, whole-gear efficiency declined from a maximum of 33% over the length range sampled. Such efficiency estimates can be used to determine catchability, which, in turn, can be used to improve the accuracy of stock assessment models when the time series of a survey is short.

Manuscript submitted 1 August 2006 to the Scientific Editor's Office.
Manuscript approved for publication 23 October 2006.
Fish. Bull. 105:278–291 (2007).

Fish density can be estimated from bottom trawl catch-per-swept-area data if there is knowledge of the whole-gear efficiency (the proportion of fish that are captured within the area spanned by the trawl doors). One approach to the estimation of whole-gear efficiency is to consider it as a function of three separate and underlying trawling processes: vertical and horizontal herding of fish, retention of fish by the net, and escapement of fish beneath the trawl footrope, which are often more tractable to field experimentation and estimation. Perhaps the earliest example of this approach was the development of a mathematical model by Dickson (1993a) for the efficiency of trawl gear in capturing fish and the application of this model for capturing Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus;* Dickson, 1993b) with the use of experimental data on herding (Engås and Godø, 1989a) and on escapement under the footrope (Engås and Godø, 1989b). Somerton and Munro (2001) proposed a modification to Dickson's (1993a) model for application to flatfish to account for the observation that flatfish herding is restricted to the length of the lower bridle that is sufficiently close to the bottom to elicit a behavioral response (Main and Sangster, 1981b). A variant of this model was then applied to seven species of North Pacific flatfish to estimate the efficiency of the capture process that was due to herding (Somerton and Munro, 2001). Although this application was followed by experiments to estimate escapement under the footrope for some of the same flatfish species (Munro and Somerton, 2002), the flatfish efficiency model was never used to combine the herding and escapement estimates and thereby produce an estimate of whole-gear efficiency. In this article, we again use the flatfish trawl efficiency model, extended by developing an estimator for the variance of efficiency, and apply the model to new experimental data for four flatfish species (flathead sole [*Hippoglossoides elassodon*], rex sole [*Glyptocephalus zachirus*], Dover sole [*Microstomus pacificus*], and arrowtooth flounder [*Atheresthes stomias*]) to estimate whole-gear efficiency for the Poly Nor'eastern trawl, which is used by the Alaska Fisheries Science Center (AFSC) on its bottom trawl surveys of the Gulf of Alaska and the Aleutian Islands region.

Materials and methods

The Poly Nor'eastern trawl

The Poly Nor'eastern trawl, pictured in Figure 1 and detailed in the Appendix, has the following basic features: the net has a four-seam design and has a 27.2-m headrope and a 36.5-m footrope equipped with 36-cm diameter bobbins to allow operation on moderately rocky terrain. The trawl doors are "V" style measuring 1.8 m by 2.7 m and weighing 816 kg each. Tailchains constructed of two 3-m

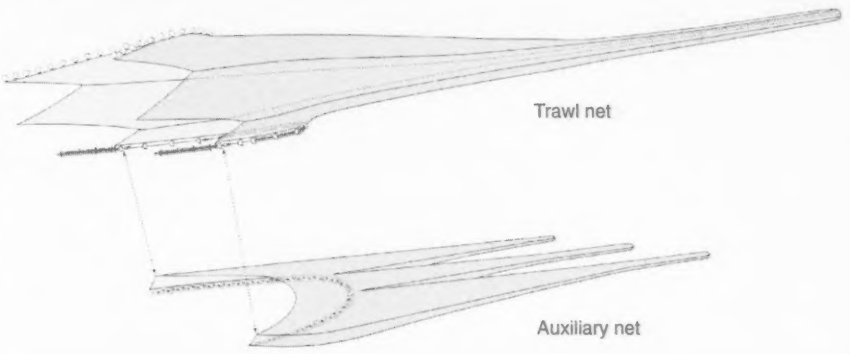


Figure 1

A diagram of the Poly Nor'eastern trawl net and the auxiliary net that was attached beneath the trawl net to capture fish escaping under the trawl footrope. Details on the construction of these nets can be found in the Appendix.

lengths of 13-mm long-link chain are joined to a single 19-mm diameter steel cable, known as the tailchain extension, that is varied in length to suit the needs of each vessel. Tailchain length is the combined length of the chain and extensions. Tailchain extensions are connected to the leading edge of each wing with three bridles measuring 54.9 m in length and constructed of 16-mm steel cable. The net mesh in the lower section of each wing ends 6.1 m behind the end of the footrope (Fig. 1; Appendix); the footrope in this section will be referred to as the wing extension.

Trawl efficiency model for flatfish

For flatfish, which are unlikely to escape through the small-mesh, codend liner, or over the headrope, the catch of a trawl (N) can be expressed as the sum of the catches of fish originating from the net and bridle paths (Dickson, 1993a; Somerton and Munro, 2001)[1]:

$$N = k_n DLW_n + k_n hDLW_{on}, \quad (1)$$

where D = fish density;
L = tow length;
W_n = the width of the net path;
W_{on} = the width of the bridle path contacted by the bridle;
k_n (net efficiency) = the proportion of fish within net path that are captured; and
h (herding coefficient) = the proportion of fish within the bridle contact path that are herded into the net path.

Because h is relative to W_{on}, which will vary with trawl design, for comparative purposes a more convenient measure of herding is the bridle efficiency (k_b) or the proportion of fish that are herded from the entire bridle path (Dickson, 1993a). Bridle efficiency can be calculated from the herding coefficient by using

$$k_b = \frac{hW_{on}}{W_d - W_n}, \quad (2)$$

where W_d = the width of the door path.
k_b = the average bridle efficiency in the area swept by the entire bridle (i.e., wing tip to door); and
h = the bridle efficiency only in the area actually contacted by the lower bridle.

Trawl efficiency (E) can then be derived from Equation 1 by dividing by the total number of fish within the door path (i.e., DLW_d).

$$E = \frac{k_n(W_n + hW_{on})}{W_d}. \quad (3)$$

Of the five quantities needed to evaluate this expression, two (W_n, and W_d) are routinely measured on bottom trawl surveys, but three (k_n, h, and W_{on}) require separate field experiments for their estimation. In this study, k_n was estimated with the data obtained from a net efficiency experiment which consisted of attaching

[1] In Somerton and Munro (2001) the parameter W_{on} in Equation 1 was instead represented by the equivalent, but more complex, expression: $W_d - W_n - W_{off}$, where W_{off} is the width of the bridle path not contacted by the bridle.

an auxiliary net under the trawl net to capture those fish escaping beneath the footrope—a method similar to that used in the studies of Engås and Godø (1989a), Walsh (1992), and Munro and Somerton (2002). Bridle efficiency (k_n) and the herding coefficient (k_n) were estimated from the data obtained from a herding experiment which consisted of repeatedly conducting trawl hauls where W_d was varied by varying the length of the bridles as has been done in the studies of Engås and Godø (1989b), Ramm and Xiao (1995), and Somerton and Munro (2001). The width of the area contacted by the bridle was estimated from the data obtained from an experiment by using bottom contact sensors to measure the off-bottom distance along the lower bridle—a distance that was reported for the Poly Nor'eastern trawl in Somerton (2003).

Net efficiency experiment

The net efficiency experiment was conducted during 2–10 July 1996 in the Gulf of Alaska, off the southeast side of Kodiak Island (58°30′N, 149°30′W) at 135–151 m depth with a 45-m chartered stern trawler, the FV *Golden Dawn*. An auxiliary net, described in the Appendix and patterned after those described in Engås and Godø (1989b) and Walsh (1992), was attached under the trawl net (Fig. 1). Trawling procedures followed normal survey protocols that included towing only during daylight hours for 15 minutes at a vessel speed of 1.5 m/sec. Catches from the trawl and the auxiliary net were kept separate, sorted by species, weighed, and all individuals were measured for total length (TL) in centimeters.

The auxiliary net, which was constructed of smaller 10.2-cm stretch mesh polyethylene netting, had a 24.8-m long headrope that was lashed directly to the fishing line of the trawl net (i.e., the forward edge of the netting) excluding the wing extension sections of the trawl footrope. The auxiliary net also had a 28.0-m long, 1.3-cm diameter chain footrope, strung with 12.7-cm rubber disks (Fig. 1), that was attached to the trawl footrope at the junctions of the roller gear and wing extensions, thus allowing the auxiliary footrope to move independently of the trawl footrope and to follow it with a separation distance of approximately 1–2 m at its center. The auxiliary net was designed so that the common intermediate section was attached to three separate codends, each having a 3.2-cm stretch mesh liner.

Experimental tows to verify that trawl performance was not altered by the attachment of the auxiliary net preceded the tows used for the measurement of net efficiency. During all of the experimental tows, a video camera, supplied with a 50 W light, was positioned in front of the footrope along the centerline of the trawl so that it had an oblique view and allowed an approximate measurement of the distance between the center of the footrope center and the sea floor. Initially, 10 tows were made with the trawl without the auxiliary net attached. When the same procedure was used for the trawl with the auxiliary net attached, the video recording indicated that the off-bottom distance of the footrope at its center was greater. By trial and error, additional weight (chain) was attached to the center of the footrope until the off-bottom distance appeared equal to that of the trawl footrope without the auxiliary net. A total of 53.4 kg of chain was attached across the centermost 6.1 m of the footrope.

Estimating k_n from the experimental data

Net efficiency, k_n, was estimated as a function of fish length, l, by fitting an analytical model to the capture probability, P (i.e., proportion of fish passing between the trawl wing tips that are caught), and fish length data pooled over tows. Four competing models, each representing a different capture process, were considered (Munro and Somerton, 2001). The first three are parametric models, which, in order of increasing complexity, are expressed as

$$\text{2-parameter logistic, } P = \frac{1}{1+e^{-(\alpha+\beta l)}}, \tag{4}$$

$$\text{3-parameter logistic, } P = \gamma\left(\frac{1}{1+e^{-(\alpha+\beta l)}}\right), \tag{5}$$

$$\text{4-parameter logistic, } P = \gamma\left(\frac{1}{1-\delta}\right)\left(\frac{1-\delta}{\delta}\right)^{\delta}\left(\frac{e^{-\delta(\alpha+\beta l)}}{1+e^{-(\alpha+\beta l)}}\right), \tag{6}$$

where α, β, γ, and δ are free parameters to be estimated.

The maximum likelihood procedure for fitting these models, detailed in Munro and Somerton (2001), was based on the assumption that the entry of individual fish into either the trawl net or the auxiliary net could be described as a binomial statistical process. The fourth model is a nonparametric model, the cubic spline, which was fitted by using an S+ (S-PLUS, Insightful Corporation, Seattle, WA) function that determined the effective number of parameters of the spline function with cross validation (Venerables and Ripley, 1994). Of the four competing models, the best fitting model was selected as the one producing the lowest value of the Akaike Information Criterion (AIC; Burnham and Anderson, 1998). Ninty-five percent confidence intervals about the capture probabilities as a function of fish length were estimated by using the bootstrapping method (Efron and Tibshirani, 1993) where entire hauls were used as the units of data resampled.

Herding experiment

The herding experiment was conducted 10–19 May 1998 aboard a 30.6-m stern trawler, the FV *Hickory Wind*, near Kodiak Island in the Gulf of Alaska at depths ranging from 126 to 183 m. A blocked sampling design was

used to minimize the effects of the spatial variation in fish density on catch. In each geographical block, three nearby, but nonoverlapping, trawl hauls were made with each of three bridle lengths (chosen in random order). Bridles lengths measured 36.6 m, 54.9 m (the standard used on AFSC bottom trawl surveys), and 73.1 m. Tailchain length was 6.1 m. Trawling was conducted during daylight hours for 30 min at 1.5 m/sec. On all hauls, door spread, wing spread, and headrope height were measured simultaneously and continuously with an acoustic trawl mensuration system. Tow length was measured as the straight-line distance between the GPS positions of the first and last footrope contact with the bottom; this distance was determined by using a bottom contact sensor (Somerton and Weinberg, 2001) attached to the center of the footrope. The catch from each haul was first sorted to species, weighed in the aggregate, and then all flatfish were measured for TL in centimeters.

Estimates of W_{on} for the three bridle lengths were calculated from the estimates of the length of bridle contact with the bottom, L_{on}, provided by the bridle contact experiment described in Somerton (2003). Although the lengths of the bridles in this experiment were the same as those in the herding experiment, the length of the tailchains was 10.4 m longer because the length of the tailchain extensions vary with the size of a vessel. Consequently, the distance between the wing tip and the door differed between experiments. Because the cable used for the tail chain extension is quite similar in diameter to that used for the bridles (i.e., 19 mm [tail chain] vs. 16 mm [bridle]), the resulting difference in length is essentially the same as a constant addition to the three bridle lengths. We assumed that the effect of such a change in total bridle length was reflected only in L_{on} and that the portion of the bridle that was off bottom, L_{off}, did not differ between the bridle measurement and herding experiments. Thus L_{on} for the herding experiment was estimated as the total bridle length (bridle length + tail chain length) for the herding experiment minus L_{off} from the bridle contact experiment. A value of W_{on} was then estimated for each bridle length as

$$W_{on} = 2\sin(\alpha) L_{on}, \tag{7}$$

where α = the average bridle angle at each bridle length during the herding experiment.

$\mathrm{Sin}(\alpha)$ was computed for each haul as

$$(W_d - W_n)/2L_t,$$

where L_t = the total length of the bridle plus the tailchain (i.e., wingtip to door distance); and
W_d and W_n = the haul mean values of door and wing spread.

Variance of W_{on} was estimated by using the delta method (Seber, 1973) and assuming no covariance between $\sin(\alpha)$ and L_{on}. This variance is expressed as

$$Var(W_{on}) = 4\left(\sin(\alpha)^2 Var(L_{on}) + L_o^2\ Var\left(\sin(\alpha)\right)\right). \tag{8}$$

$\mathrm{Var}(\sin(\alpha))$ for each bridle length was calculated as the between-haul variability in $\sin(\alpha)$, and $\mathrm{Var}(L_{on})$ was obtained from Somerton (2003).

Estimating *h* from the experimental data

The herding coefficient was estimated by fitting a modified version of Equation 1 to the experimental data on W_n, W_{on}, and catch (in numbers). The first modification, which is considered more fully in Somerton and Munro (2001), consists of introducing a new parameter, k, defined as the product of D and k_n, that is allowed to vary among blocks. The second modification is to allow length dependency in k and h. The modified equation is

$$N_{ijk} = k_{ik}(LW_n)_{ij} + k_{ik}h_k(LW_{on})_{ij} + \varepsilon_{ijk}, \tag{9}$$

where subscript i refers to block number, j to bridle length within block, k to fish length class, and ε_{ijk} is a normally distributed error term.

For each fish-length class, fitting Equation 9 to the herding data required estimation of n+1 parameters, where n is the number of blocks sampled (i.e., a unique value of k for each block and a common value of h for all blocks). Because the model is nonlinear in the parameters (h and k are multiplied together), it was fitted to data by using nonlinear regression (Venables and Ripley, 1994). Fish length classes used in the calculations were chosen such that the number of observations of length was approximately equal among classes, and differed among species due to differences in the number and size range of sampled fish. After h was estimated, k_b was calculated for the standard bridle length with Equation 2.Variance of k_b was estimated by using a bootstrapping process designed to include among-block variability in catch and trawl measurements as well as the uncertainty in the estimated value of W_{on}. First, a bootstrap replicate of catch and trawl measurement data was obtained by randomly choosing, with replacement, blocks of data, each containing a single haul at each bridle length, from the n blocks sampled (blocks rather than hauls were randomized to preserve the within-block correlation in catch). Second, for each bridle length, a value of W_{on} was computed by using a normal random number generator with values of the mean and variance of W_{on} reported in Somerton (2003). Third, h was then estimated by fitting Equation 9 by using nonlinear regression, and k_b was estimated from h by using Equation 2. Fourth, the process was repeated 100 times and the variance of k_b was estimated as the variance among the replicates. Although the model that we used allows for length-dependent herding, herding may not be a length-dependent process in all species. To determine if k_b varied with fish length, the estimated length-specific values of k_b were regressed on the midpoints of the length intervals.

Table 1

Selectivity model selection and estimated parameters of the best fitting model. The value of the Akaike Information Criterion (AIC) is shown for each of four possible models described in Munro and Somerton (2001): 2-parameter logistic, 3-parameter logistic, 4-parameter logistic, and cubic spline models. The estimated parameters of the best fitting model, that is, the one with the lowest value of the AIC, are shown. Parameter notation (α,β,γ) is the same as in Equations 4–6 in the text. Although, for arrowtooth flounder (*Atheresthes stomias*) the best fitting model is the cubic spline, the parameters of the best fitting parametric model are also included for use at lengths >20 cm.

	AIC				Estimated parameters		
Species	2-parameter logistic	3-parameter logistic	4-parameter logistic	Cubic spline	α	β	γ
Arrowtooth flounder (*Atheresthes stomias*)	6568.8	6502.0	6504.0	6382.7	−2.65	0.156	0.966
Flathead sole (*Hippoglossoides elassodon*)	1804.3	1794.7	1796.7	1863.4	−3.66	0.208	0.861
Rex sole (*Glyptocephalus zachirus*)	1642.8	1594.0	1596.0	1634.9	−7.45	0.376	0.873
Dover sole (*Microstomus pacificus*)	1245.9	1247.9	1249.9	1256.6	2.27	−0.055	

Estimating whole-gear efficiency

Estimates of trawl efficiency, by 1 cm length categories, were obtained by substituting into Equation 3 the estimates of mean W_n and W_d for the standard bridle length from the herding experiment, k_n from the net efficiency experiment, h from the herding experiment, and W_{on} from the bridle measurement experiment. Variance of E, which was derived from Equation 2 by using the delta method (Seber, 1973) and by assuming no covariance between any of the parameters, was calculated as

$$V(E)=\left(\frac{W_n+hW_{on}}{W_d}\right)^2 V(k_n)+\left(\frac{k_n}{W_d}\right)^2 V(W_n)+$$
$$\left(\frac{k_nW_{on}}{W_d}\right)^2 V(h)+\left(\frac{k_nh}{W_d}\right)^2 V(W_{on})+ \qquad (10)$$
$$\left(\frac{k_n(W_n+hW_{on})}{W_d^2}\right)^2 V(\ _d).$$

The variance variables $V(W_n)$, and $V(W_d)$ were estimated as the variance of these dimensions during the herding experiment. Variance variables $V(k_n)$, $V(h)$, and $V(W_{on})$ were calculated as described earlier.

Results

Net efficiency experiment

All four species of flatfish were present in each of the 34 tows successfully completed. Total number and size range of measured fish were the following: 9512; 5–84 cm TL (arrowtooth flounder); 1701; 6–45 cm TL (flathead sole); 2142; 10–61 cm TL (rex sole); and 949; 30–57 cm TL (Dover sole).

Estimates of k_n

The best fitting model of k_n as a function of length differed among the four flatfish species. For arrowtooth flounder, the best fitting model was the cubic spline (Table 1, Fig. 2), primarily because of its flexibility to fit the selectivity of small (<20 cm TL) fish. At larger sizes (>20 cm TL), however, the best fitting parametric model was the 3-parameter logistic model. The cubic spline model fitted almost equally well (Fig. 2); therefore, we have also included the parameter estimates of this model in Table 1. For flathead sole and rex sole, the best fitting selectivity model was the 3-parameter logistic with a maximum capture probability substantially below that for arrowtooth flounder (Table 1; Fig. 2), indicating that the escapement beneath the footrope for these species is substantial even at the largest sizes. For Dover sole, the best fitting model was the 2-parameter logistic model, with the parameters chosen such that the predicted capture probability decreased monotonically, and nearly linearly, over the observed length range of fish.

Herding experiment

Seventeen geographic blocks, each containing three hauls, were successfully completed. For arrowtooth flounder, 11,510 fish were measured and all 17 blocks had nonzero catches at all bridle lengths. For the remaining species, the statistics are as follows: flathead sole (6632 measurements, 17 blocks), rex sole (620 measurements, 13 blocks), and Dover sole (392 measurements, 12 blocks).

The width of the area contacted by the bridles (W_{on}) increased dramatically with increasing bridle length (Table 2), primarily because of the increase between the short and standard bridle length. At the shortest bridle length, the estimated value of W_{on} indicated that the lower bridle was typically lifted off the bottom along its entire length. Other aspects of trawl geometry changed with increasing bridle length. Wingspread

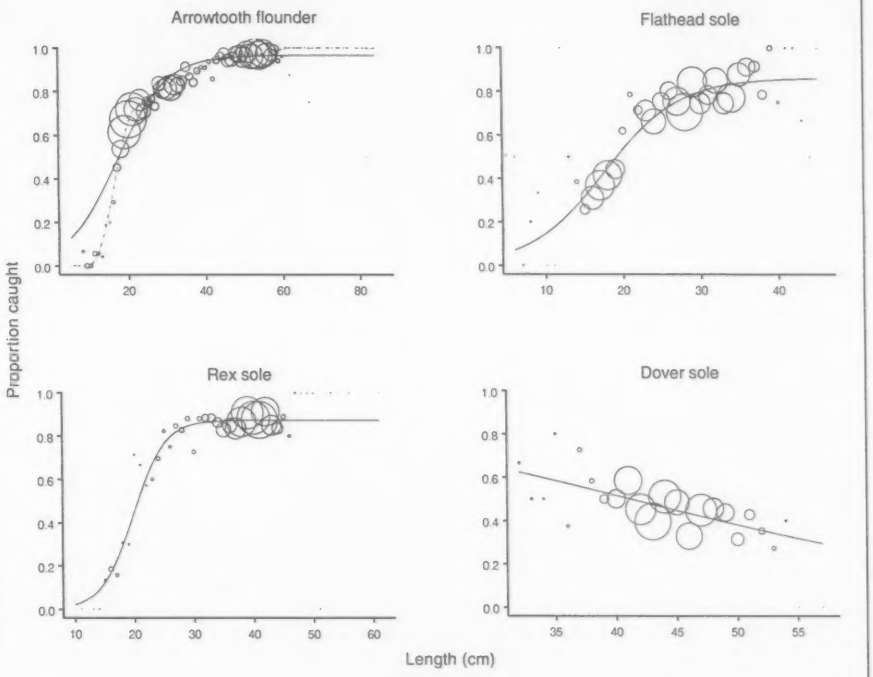


Figure 2

Proportion caught as a function of body length for four species of flatfish: arrowtooth flounder (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), rex sole (*Glyptocephalus zachirus*), and Dover sole (*Microstomus pacificus*). For each species, the fit of the best fitting parametric model is shown with a solid line. However, for arrowtooth flounder (*Atheresthes stomias*), a nonparametric model, the cubic spline, fitted the data even better and is shown with a dashed line. Relative abundance by size group is indicated by the radius of the circles.

decreased slightly (0.4 m; Table 2) as bridle length increased, but the decrease was not significant; bridle angle (i.e., the angle between the bridles and the direction of travel (α) decreased significantly with increasing bridle length.

Estimates of k_b

Tests for length dependency in the herding process, based on the linear regression of k_b on fish length, indicated that the slopes were positive in all four cases (Table 3; Fig. 3), but significant only for arrowtooth flounder. Because the significance of the relationship for arrowtooth flounder is primarily due to the conspicuously lower value of k_b at the smallest length class (Fig. 3), we consider the evidence for an increase in k_b with size as credible, but still equivocal.

Length dependency in the herding process should lead to differences in the size distribution as bridle length is changed; however, size distributions for each species appeared quite similar for each of the three bridle lengths (Fig. 4) and none of the species had a significant ($P<0.05$) difference in mean size among bridle lengths. Consequently, k_b was considered as length invariant in the calculation of efficiency for all four species.

Length-invariant estimates of k_b were similar for the three sole species, ranging from 0.22 for rex sole to 0.24 for Dover sole (Table 4). These values are slightly larger than the estimated value of 0.17 for arrowtooth flounder. The values of the herding coefficient (h), or the herding efficiency in relation to the area swept by the lower bridle, were considerably higher than the values of k_b. For the three sole species, h ranged from 0.53 for rex sole to 0.58 for Dover sole. Again, these values were higher than the h estimate of 0.39 for arrowtooth flounder. Thus, roughly 40–50% of the flatfish encountering the lower bridle were ultimately herded into the path of the net.

Whole-gear trawl efficiency

Trawl efficiency estimates for arrowtooth flounder, flathead sole, and rex sole increased with increasing fish length and reached maxima of 0.45, 0.42, and 0.43,

Table 2

Trawl configuration parameters for the herding experiment. Included are the bridle lengths that were used, the means (and standard deviations) of the door width (W_d), wing width (W_n), bridle angle (α), bridle width (W_d–W_n), and bridle width in contact with the bottom (sea floor) (W_{on}).

Bridle length (m)	Door width (m) W_d	Wing width (degrees) W_n	Bridle angle (m) α	Bridle width (m) $W_d - W_n$	Bridle width on bottom (m) W_{on}
73.1	54.1 (3.4)	15.9 (0.6)	13.9 (1.0)	38.2 (2.8)	16.7 (2.1)
54.9	47.8 (2.7)	16.1 (0.6)	15.0 (1.0)	31.6 (2.1)	13.5 (2.5)
36.6	39.8 (1.8)	16.3 (0.5)	16.0 (1.0)	23.5 (1.4)	0.0 (0.0)

Table 3

Fit of a linear model to estimates of the bridle herding coefficient (k_b) as a function of fish length. The number of fish length bins, the slope of the regression line fit to k_b and length data, and the probability that the slope equaled zero is shown for each species. Significance of the slope ($P<0.05$) indicates that herding changes with fish size.

Species	Number of length bins	Slope of regression line	P(slope=0)
Arrowtooth flounder (*Atheresthes stomias*)	8	0.0035	0.039
Flathead sole (*Hippoglossoides elassodon*)	6	0.0033	0.616
Rex sole (*Glyptocephalus zachirus*)	5	0.0057	0.554
Dover sole (*Microstomus pacificus*)	4	0.0184	0.150

Table 4

Estimates of r^2 for the fit of the model (Eq. 9) without length dependency, and the values of h, k_b (Eq. 2), and the standard deviation (SD) of K_b for each of the four species of flatfish.

Species	r^2	h	k_b	SD(k_b)
Arrowtooth flounder (*Atheresthes stomias*)	0.71	0.391	0.167	0.038
Flathead sole (*Hippoglossoides elassodon*)	0.98	0.555	0.237	0.047
Rex sole (*Glyptocephalus zachirus*)	0.84	0.531	0.222	0.066
Dover sole (*Microstomus pacificus*)	0.62	0.576	0.239	0.162

respectively (Fig. 5), indicating that slightly more than 40% of the largest individuals that passed between the doors of the trawl were ultimately caught. In contrast, the efficiency estimates for Dover sole were considerably lower over the sampled size range and monotonically decreased with increasing fish length.

Discussion

Net efficiency

For three of the four flatfish species (i.e., arrowtooth flounder, flathead sole, rex sole), net efficiency (k_n) increased monotonically with fish size. For Dover sole, however, net efficiency declined over the sampled size range and was considerably lower than that for the other species in the larger commercial sizes. This unusual pattern is likely the result of two factors. First, small individuals, which are likely better at escaping under the footrope, were not sampled; consequently, the left-hand, ascending, portion of the selection curve is not defined. Second, the decline in capture probability with increasing size indicates that this species is behaviorally more adept at escaping under the footrope, probably by swimming ahead of the footrope, then dropping to the bottom, and allowing the footrope to pass over. Although distinct species-specific escape responses to a footrope

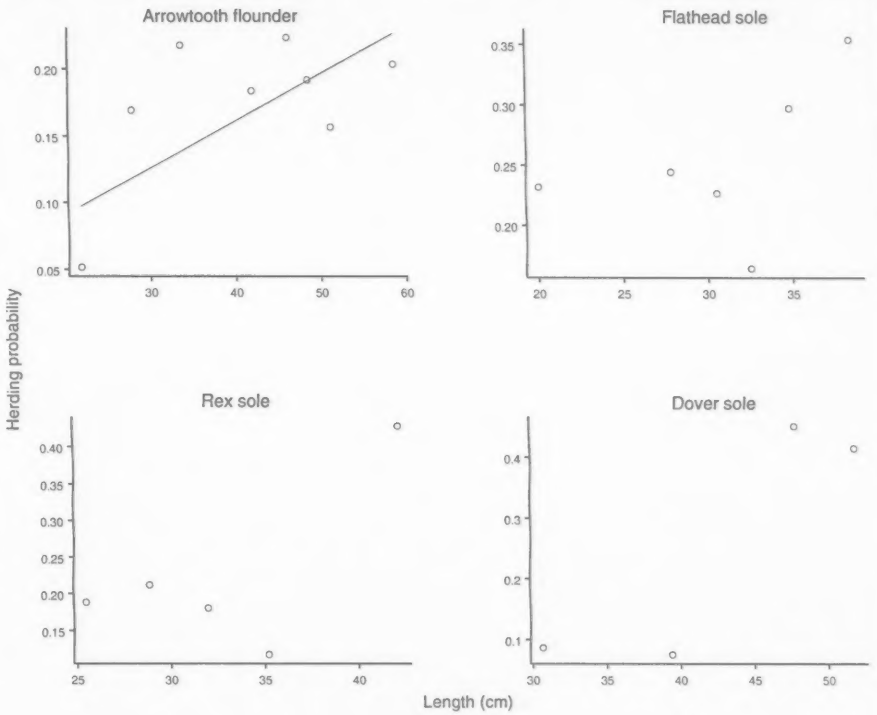


Figure 3

The herding probability (h) plotted against fish length for four species of flatfish: arrowtooth flounder (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), rex sole (*Glyptocephalus zachirus*), and Dover sole (*Microstomus pacificus*). The herding probably increased significantly with length only for arrowtooth flounder (*Atheresthes stomias*). This relationship is shown with a solid line.

have been reported (Bublitz, 1996), our video recordings were insufficiently clear for us to distinguish species and therefore we could not determine the mechanism leading to the decline in capture probability. Regardless of the mechanism, a decline in net efficiency with increasing size has been previously reported for another flatfish (i.e., yellowtail flounder, *Limanda ferruginea*; Walsh, 1992).

Assumptions with the net efficiency experiment

The auxiliary net did not extend across the full width of the trawl net, but only across the center 78% of the width where the mesh of the trawl net attaches to the footrope. Our use of the estimated net efficiency in this section as a proxy for that of the total net spread, which is measured at the junction of the upper bridle and wing tip, is based on the assumption that the average escapement in the unsampled section is the same as that in the sampled section. From video observations (K. Weinberg, unpubl. data), it is evident that flatfish encountering these outer portions of the footrope tend to be herded toward the center of the footrope rather than pass under or over the footrope. Although we have no quantitative data on the change in escapement rate across the width of the trawl, we believe that our extrapolation of the measured escapement rate into the unsampled portion of the net spread potentially results in a slight underestimate of net efficiency.

Herding

One would expect herding to be a length-dependent process because the swimming endurance of fish, and therefore their ability to maintain position in front of the bridle, increases with body size (Winger et al., 1999). Our evidence for length-dependent herding, however, is equivocal. All four of the species had a positive slope in the regression of k_b on body length (Table 2), but in only one case, arrowtooth flounder, was

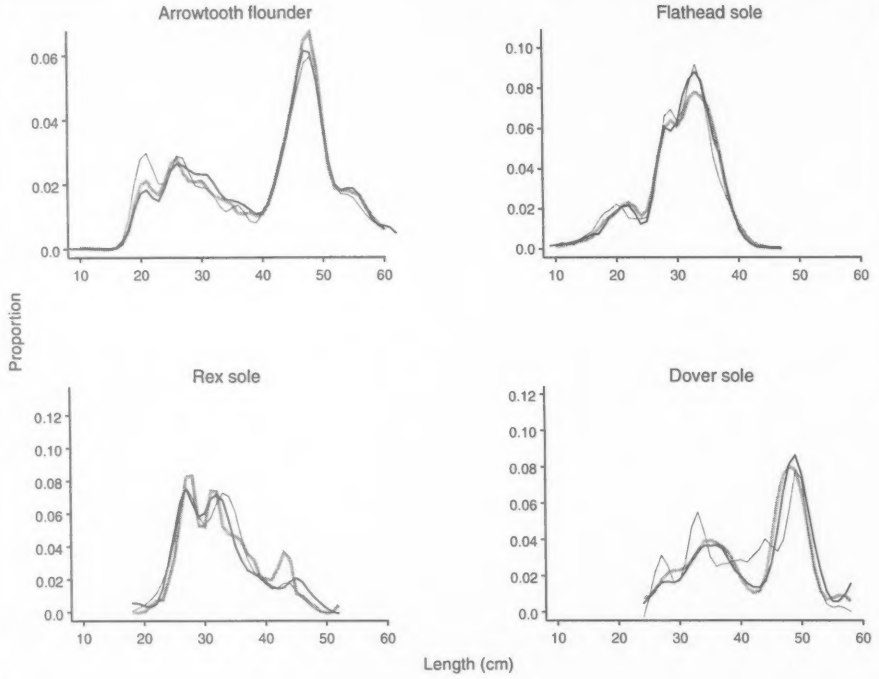


Figure 4

Length-frequency distributions, expressed as the proportion caught at each length, for each of the four flatfish species (arrowtooth flounder (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), rex sole (*Glyptocephalus zachirus*), and Dover sole (*Microstomus pacificus*)) averaged over all hauls taken in the herding experiment are shown for three bridle lengths: short (thin line), standard (medium line), and long (thick line).

the slope statistically significant and this significance was dependent on the relatively low value of k_b in the smallest size interval. In previous studies, evidence for length-dependent herding has been inconsistent. Although Engås and Godø (1989a) observed increases in bridle efficiency with fish length for Atlantic cod and haddock, Somerton and Munro (2001) found either no change or decreases in bridle efficiency for seven species of flatfish, and Ramm and Xiao (1995) found no evidence of length dependent herding for any of a variety of species.

An alternative way of detecting length-dependent herding is through the changes in mean length of the catch as bridle length is changed, because the processes leading to the differences in herding ability with fish size would be intensified with increases in bridle length. Although Engås and Godø (1989a) and Andrew et al. (1991) found an increase in fish length with increasing bridle length, Somerton and Munro (2001) found a decrease in fish length. Because, in the present study, we observed no significant changes in mean size with bridle length (Fig. 4), even for arrowtooth flounder, which had a significant increase in k_b with length, length-dependency in the herding process is, at best, weak for flatfish sampled with the Poly Nor'eastern trawl and is therefore unlikely to contribute substantially to size selectivity.

Although estimates of k_b for the four species were pairwise not significantly different from each other, the estimates for flathead sole, rex sole, and Dover sole were very similar (Table 3), but considerably greater than the estimate for arrowtooth flounder. From an ecological perspective, similarity in the herding coefficients for the three sole species makes sense because all eat sessile or slow moving prey taken from the bottom and are likely relatively slow swimmers that stay close to the bottom when herded, whereas arrowtooth flounder eats relatively large pelagic fish (Yang and Nelson, 2000) and is likely a stronger, more agile swimmer that readily leaves the bottom.

The k_b estimates for the three sole species are also quite similar to the estimates that we obtained previously for the 83-112 Eastern trawl (flathead sole, 0.24; rex sole, 0.22; Dover sole, 0.27; Somerton and Munro,

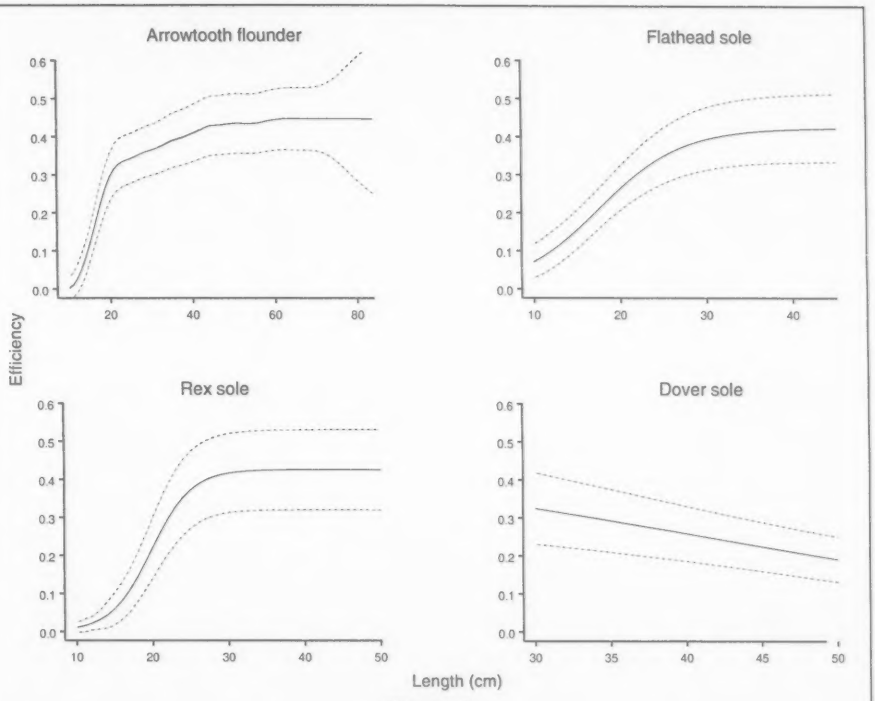


Figure 5

Whole-gear efficiency (solid line), and 95% confidence intervals (dotted lines), as a function of fish length for each of the four flatfish species: arrowtooth flounder (*Atheresthes stomias*), flathead sole (*Hippoglossoides elassodon*), rex sole (*Glyptocephalus zachirus*), and Dover sole (*Microstomus pacificus*).

2001). Although the two trawls have bridles that are identical in length and thickness, we found the similarity in the k_b estimates surprising because the bridles on the Poly Nor'eastern trawl are obscured over their entire length by mud clouds during trawling (Somerton, 2003), whereas those on the 83-112 Eastern trawl are mostly unobscured and likely visible to fish. This indicates that either the lower bridle, even in a mudcloud, is more visible to a flatfish than it seems to be when viewed with a video camera or that visibility of the lower bridle is not particularly important for flatfish herding—at least for the type of bridles used on AFSC bottom survey trawls.

For flathead, rex, and Dover sole, 55% (average value of h) of the individuals within the bridle contact path and 23% of the individuals within the entire bridle path were herded into the net path. Assuming that herded fish have the same probability of being captured as fish originally in the net path, then the herded fish comprise about 32% of the catch. For arrowtooth flounder, herded fish comprise 25% of the catch. This finding indicates that herding contributes substantially to the catch of these species and cannot be ignored when computing swept area estimates of abundance.

Assumptions with the herding experiment

The objective of the herding experiment was to change the size of the area experiencing a herding stimulus without altering other aspects of trawl geometry or performance. However, as in our previous experiment (Somerton and Munro, 2001), and those of Ramm and Xiao (1996) and Engås and Godø (1989a), both the net width and the bridle angle changed in response to the change in bridle length (Table 2). Because of these unintended changes in trawl geometry, the width of the bridle area did not change in proportion to the change in bridle length. Thus, the increase in the width of the bridle path (i.e., W_d–W_n) was 8.1 m between the short length and standard length bridles, but only 6.6 m between the standard length and the long length bridles. A better design for a herding study would be one in which the incremental changes in bridle path width, or, better yet W_{on}, were approximately equal among bridle lengths. By studying bridle geometry as a function of bridle length, it should be possible to choose the correct experimental bridle lengths to achieve this equality.

One assumption with the herding model is that flatfish are stimulated to herd by the bridles only from the

footrope attachment of the lower bridle out to a distance L_{on}, but not beyond. This is an over simplification of the herding process, but in our previous study (Somerton and Munro, 2001) video recordings substantiated this assumption. Because the bridles are obscured by the mudclouds on the Poly Nor'eastern trawl, not only were we unable to verify the fish reaction to the bridles but the mud clouds themselves may have provided a herding stimulus as they reportedly do for some roundfish (Main and Sangster, 1981a, 1981b). If so, the effective length of the bridle over which herding occurs could be longer than L_{on}. We attempted to answer this question by positioning a video camera to allow us to observe flatfish behavior at the inner edge of the mud cloud, but were unsuccessful.

Another assumption is that the estimates of L_{on} can be extrapolated from the bridle measurement experiment to the herding experiment. On all vessels that we use for experiments, the tailchain extensions are adjusted in length depending on the size of the vessel and storage location of the doors when out of water. On the herding and bridle measurement experiments, the difference in the sizes of the vessels was so large that the tailchain length was approximately 10 m longer in the bridle measurement experiment. Because the cable used for the tail chain extensions is quite similar in diameter to that used for the bridles (i.e., 19 vs. 16 mm), the difference in tailchain length can be viewed as an equivalent difference in bridle length. Although unsubstantiated, our belief is that the combined forces on the lower bridle are such that a lengthening of the bridle by 10 m would result in a minimal change in the length of the bridle held off the bottom and therefore simply add a 10-m increment to L_{on}.

Whole-gear efficiency

We are aware of two previous studies in which whole-gear efficiency and the efficiency of the subsidiary trawling processes were experimentally estimated. One of these studies, that of Dickson (1993b), focused on Atlantic cod and haddock and therefore produced results that were not directly comparable to ours. The other, that of Harden Jones et al. (1977), is comparable because it was focused on a flatfish (plaice, *Pleuronectes platessa*) and used a bottom trawl similar in design to the Poly Nor'eastern trawl. In the latter study, gear efficiency was estimated by determining the fate (i.e., capture or escape) of individual fish tagged with acoustic transponders which allowed them to be located with a sector scanning sonar. For all fish passing between the doors, 44% were subsequently caught. This result is quite similar to the maximum efficiency of the Poly Nor'eastern trawl for three of the species in our study (mean=43%). In the Harden Jones et al. (1977) study, fish entering the trawl within the bridle path (between the wings and doors) had a 22% chance of being caught and fish entering the trawl within the net path had a 61% chance of being caught. Again, based on the maximum efficiency of the Poly Nor'eastern trawl, there was a 19% mean chance of being caught (calculated as $k_b k_n$) for fish entering the trawl within the bridle path and a 90% chance of being caught for fish entering the net path. Thus, compared with the Harden Jones et al. (1977) study, the bridle efficiency of the Poly Nor'eastern trawl for flatfish was less, net efficiency was greater, but the whole-gear efficiency was nearly the same.

For some bottom trawl surveys, including those conducted by the AFSC, swept area calculations are based on wing spread rather than door spread and the selectivity or catchability parameters in stock assessment models are formulated according to this convention. To convert efficiency estimates presented here to the estimates appropriate for the net spread convention, the values must be multiplied by the quotient of the door spread and net spread, which for the Poly Nor'eastern trawl is approximately equal to 3 (47.8 m/16.1 m).

Such efficiency estimates can be used to estimate survey catchability, which, in turn, can be used to constrain the survey catchability parameter in stock assessment models. In situations when the survey time series is relatively short, constraining the catchability parameter can lead to improved predictions of stock biomass and harvest rate (Somerton et al., 1999).

Literature cited

Andrew, N. L., K. J. Graham, S. J. Kennelly, and M. K. Broadhurst
1991. The effects of trawl configuration on the size and composition of catches using benthic prawn trawls off the coast of New South Wales, Australia. ICES J. Mar. Sci. 48:201–209.

Bublitz, G. G.
1996. Quantitative evaluation of flatfish behavior during capture by trawl gear. Fish. Res. 25:293–304.

Burnham, K. P., and D. R. Anderson
1998. Model selection and inference: practical information-theoretic approach, 353 p. Springer-Verlag, New York, NY.

Dickson, W.
1993a. Estimation of the capture efficiency of trawl gear. I: development of a theoretical model. Fish. Res. 16: 239–253.
1993b. Estimation of the capture efficiency of trawl gear. II: testing a theoretical model. Fish. Res. 16: 255–272.

Efron, B., and R. Tibshirani
1993. An introduction to the bootstrap, 436 p. Chapman and Hall, New York, NY.

Engås, A., and O. R. Godø
1989a. The effect of different sweep lengths on the length composition of bottom-sampling trawl catches. J. Cons. Int. Explor. Mer 45:263–268.
1989b. Escape of fish under the fishing line of a Norwegian sampling trawl and its influence on survey results. J. Cons. Int. Explor. Mer 45:269–276.

Harden Jones, F. R., A. R. Margetts, M. G. Walker, and G. P. Arnold
1977. The efficiency of the granton otter trawl determined by sector-scanning sonar and acoustic transponding tags. Rapp. P-v. Reun. Cons. Explor. Mer 170:45–51.

Main, J., and G. I. Sangster
1981a. A study of the sand clouds produced by trawl boards and their possible effect on fish capture. Scott. Fish. Res. Rep. 20:1–20.
1981b. A study of the fish capture process in a bottom trawl by direct observations from a towed underwater vehicle. Scott. Fish. Res. Rep. 23:1–23.
Munro, P. T., and D. A. Somerton
2001. Maximum likelihood and non-parametric methods for estimating trawl footrope selectivity. ICES J. Mar. Sci. 58:220–229.
2002. Estimating net efficiency of a survey trawl for flatfishes. Fish. Res.55:267–279.
Ramm, D. C., and Y. Xiao
1995. Herding in groundfish and effective pathwidth of trawls. Fish. Res. 24:243–259.
Seber, G. A. F.
1973. The estimation of animal abundance, 343 p. Hafner Press, New York, NY.
Somerton, D.
2003. Bridle efficiency of a survey trawl for flatfish: measuring the length of the bridles in contact with the bottom. Fish. Res. 60:273–279.
Somerton, D. A., and P. Munro
2001. Bridle efficiency of a survey trawl for flatfish. Fish. Bull. 99:641–652.
Somerton, D. A., and K. L. Weinberg
2001. The affect of speed through the water on footrope contact of a survey trawl. Fish. Res. 53:17–24.
Somerton, D., J. Ianelli, S. Walsh, S. Smith, O. R. Godø, and D. Ramm.
1999. Incorporating experimentally derived estimates of survey trawl efficiency into the stock assessment process: a discussion. ICES J. Mar. Sci. 56:299–302.
Venerables, W. N., and B. D. Ripley
1994. Modern applied statistics with S-plus, 462 p. Springer-Verlag, New York, NY.
Walsh, S. J.
1992. Size-dependent selection at the footgear of a groundfish survey trawl. N. Am. J. Fish. Manage. 12: 625–633.
Winger, P. D., P. He, and S. J. Walsh
1999. Swimming endurance of American plaice (*Hippoglossoides platessoides*) and its role in fish capture. ICES J. Mar. Sci. 56:252–265.
Yang, M. S., and M. W. Nelson
2000. Food habits of the commercially important groundfishes in the Gulf of Alaska in 1990, 1993, and 1996. NOAA Tech. Memo. NMFS-AFSC-112, 174 p.

Appendix

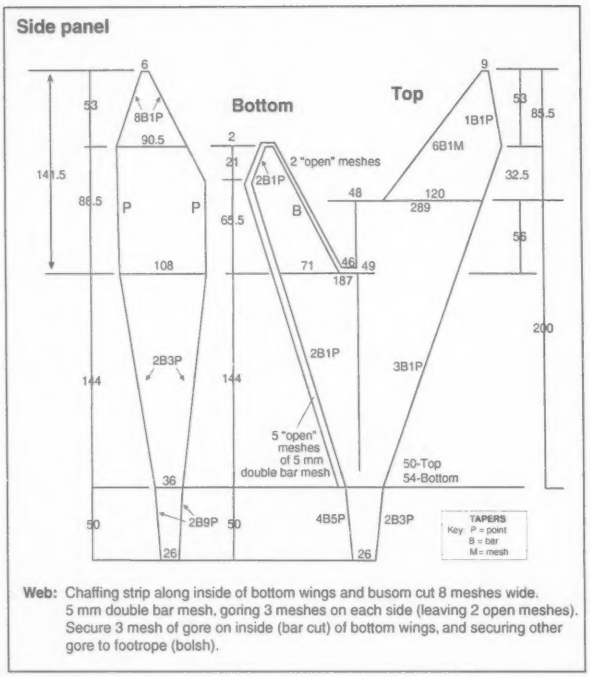
Description and construction diagram for the trawl and the auxiliary net

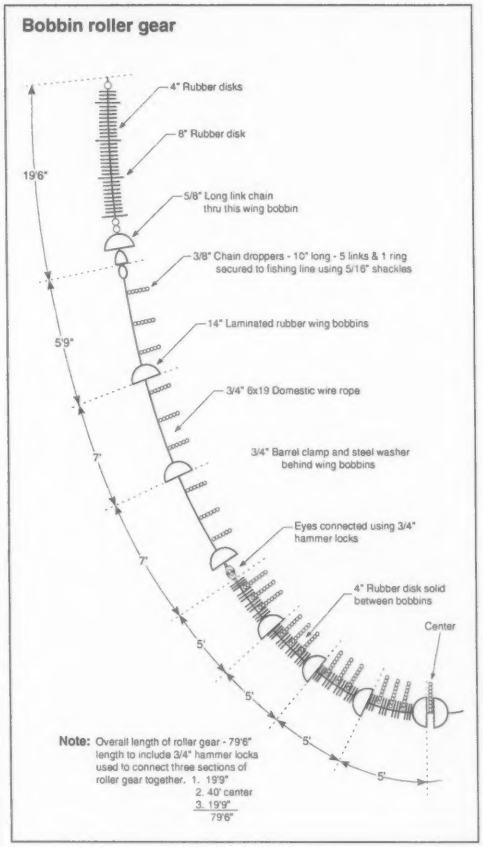
Poly Nor'eastern survey bottom trawl The Poly Nor' eastern is a high-rise, 4-seam, trawl rigged with rubber bobbin roller gear designed for use on moderately rocky terrain (Appdx. Fig.1). The net is constructed of 12.7-cm stretched-mesh polyethylene web (4-mm thickness top and sides, 5-mm thickness in the bottom and intermediate sections) and has a double 8.9-cm (4-mm thickness) codend with a 3.2-cm nylon mesh liner. The 27.2-m headrope supports twenty 30.5-cm diameter and four 20.3-cm diameter trawl floats that provide 220 kg of total lift. The webbing is hung from a 24.9-m bolsh line consisting of 0.95-cm diameter bare stranded wire wrapped with 0.95-cm diameter polypropylene rope, that attaches to a 24.7-m chain (1.6-cm long-link) fishing line. The 24.2-m, 1.9-cm diameter stranded-wire footrope is rigged with three sections of roller gear that attach to the fishing line with 25-cm pieces of 0.95-cm chain. The 12.2-m center section of the roller gear consists of eight 36-cm rubber bobbins separated by 10-cm rubber disks. To either side of the center segment is a 6.0-m section that consists of four 36-cm rubber bobbins separated by pieces of rubber hose to protect the wire footrope. In addition, 5.9-m footrope wing extensions consisting of 1.9-cm diameter stranded-wire rope with 10-cm and 20-cm rubber disks span the lower "flying" wing section on each side of the net. Riblines, constructed of 1.9-cm diameter Duralon 2 in 1 braided rope (Samson Inc., Ferndale, WA), are hung along 98% of the stretched length of the netting.

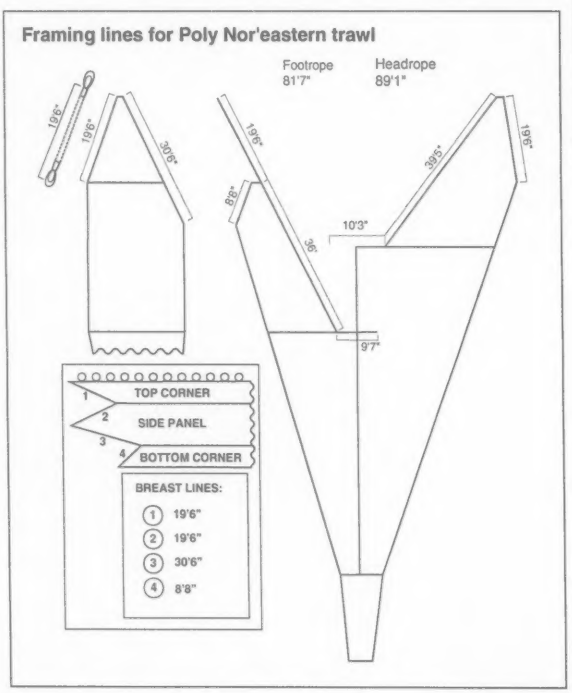
The net is connected to a pair of 1.8×2.7 m steel "V" doors, weighing approximately 816 kg each, by two 3-m door legs, consisting of 1.6-cm long-link chain; a 12.2-m door leg extension, consisting of 1.9-cm diameter bare stranded wire; and triple 54.9-m bridles, consisting of 1.6-cm diameter bare stranded wire, on each side of the net. Additional 46-cm and 23-cm-long extensions, consisting of 1.3-cm long-link chain, connect the upper and middle bridles to the respective wing tips of the trawl.

Auxiliary net for Poly Nor'eastern trawl gear The auxiliary net is a 2-seam trawl fitted with small side panels designed to help maintain steady footrope contact with the bottom during periods of intermittent contact by the Poly Nor'eastern footrope; it also fitted with three codends for catch retention should the net sustain damages (Appdx. Fig. 2). The 24.8-m headrope, constructed of 1.9-cm diameter double braid polyester rope, is lashed to the survey trawl bolsh line. The 28.0-m footrope, constructed of 1.3-cm long-link chain passing through 12.7-cm diameter rubber disks, is lashed to the 1.9-cm diameter double braid polyester fishing line from which the netting is hung. A delta plate located just aft of each survey trawl wing extension is used to connect both the front ends of the headrope and the fishing line to the trawl footrope.

With the exception of the 8.9-cm stretched-mesh codends, the net is constructed of 10.2-cm stretched-mesh polyethylene web (4 mm in body and codend and 5 mm in the wings and mouth area of the lower panel). For added protection, netting was doubled on the leading wing edges of the upper panel, the wings and mouth areas of the lower panel, the forward meshes of the side panels, the aft 10 meshes of the intermediate section, and throughout the codends. Riblines, constructed of 1.6-cm diameter poly dacron twisted rope, were hung along 92.5% of the stretched length of the netting.

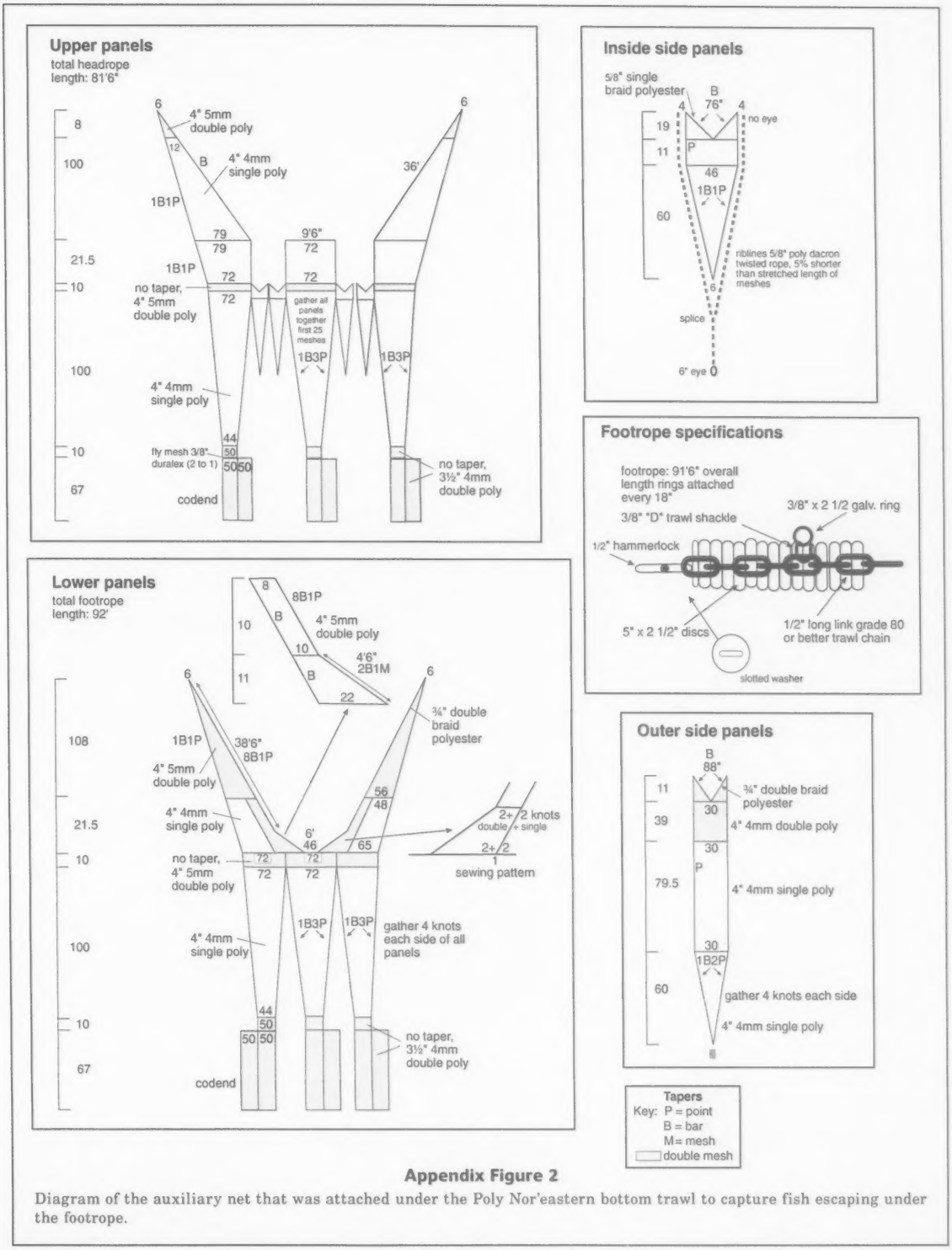



Bobbin roller gear
4" Rubber disks
8" Rubber disk
19'6"
5/8" Long link chain thru this wing bobbin
3/8" Chain droppers - 10" long - 5 links & 1 ring secured to fishing line using 5/16" shackles
14" Laminated rubber wing bobbins
5'9"
3/4" 6x19 Domestic wire rope
3/4" Barrel clamp and steel washer behind wing bobbins
7'
Eyes connected using 3/4" hammer locks
7'
4" Rubber disk solid between bobbins
Center
5'
5'
5'
5'
Note: Overall length of roller gear - 79'6" length to include 3/4" hammer locks used to connect three sections of roller gear together. 1. 19'9" 2. 40' center 3. 19'9" 79'6"



Appendix Figure 1

Diagram of the Poly Nor'eastern bottom trawl.



Appendix Figure 2

Diagram of the auxiliary net that was attached under the Poly Nor'eastern bottom trawl to capture fish escaping under the footrope.

Yellow (*Perca flavescens*) and Eurasian (*P. fluviatilis*) perch distinguished in fried fish samples by DNA analysis

Rex M. Strange

Carol A. Stepien (contact author)

Email address for C. A. Stepien: Carol.Stepien@utoledo.edu

Great Lakes Genetics Laboratory
Lake Erie Center and Department of Environmental Sciences
The University of Toledo
6200 Bayshore Road
Toledo, Ohio 43618

DNA techniques are increasingly used as diagnostic tools in many fields and venues. In particular, a relatively new application is its use as a check for proper advertisement in markets and on restaurant menus. The identification of fish from markets and restaurants is a growing problem because economic practices often render it cost-effective to substitute one species for another. DNA sequences that are diagnostic for many commercially important fishes are now documented on public databases, such as the National Center for Biotechnology Information's (NCBI) GenBank.[1] It is now possible for most genetics laboratories to identify the species from which a tissue sample was taken without sequencing all the possible taxa it might represent.

We were contacted by reporters from a news agency, who were interested in determining whether yellow perch "fish fries" in their local restaurants were, in fact, local yellow perch (*Perca flavescens* Mitchell) taken from the Great Lakes. In recent years it has become economically desirable to substitute Eurasian perch (*P. fluviatilis* Linnaeus) or some other species for yellow perch because of the decline of stocks of yellow perch in the Great Lakes and because of rising prices, both of which raise truth-in-advertising questions. Such cases of substitution usually involve replacement with less expensive fish species, which are difficult to detect in fillets (see Ward, 2000).

We agreed to attempt to identify the fish using DNA techniques because the Great Lakes Genetics Laboratory has several on-going projects involving evolutionary genetics of yellow perch and other percids (e.g., Faber and Stepien, 1997; Ford and Stepien, 2004). However, instead of the fresh frozen fillets that we expected, the reporters sent us breaded and deep fried fish fillets taken from served dinners. We decided to attempt to identify the species of the fish, despite our initial misgivings as to whether useful amounts of DNA could be extracted from deep-fried material. In the present study, we outline a procedure with molecular tools and an analysis that allows the identification of any species for which sequences are documented on GenBank.[1]

Materials and methods

We removed approximately 10 mg of muscle tissue from below the breading of each fried fillet, submerged the tissue in an ethanol (95%) wash, and allowed the wash to sit overnight at room temperature. No other attempt was used to remove any residual cooking oil. Samples were then air-dried before digestion with proteinase K. After complete digestion, DNA was isolated by using standard phenol-chloroform extractions, alcohol precipitation, and two washes with 70% ethanol. From experience, we found that the final pellet of DNA was smaller than the DNA yield we would expect from uncooked material; therefore we suspended the pellet with 30 µL (microliters) of dd (deionized distilled) H_2O rather than the 100 µL we typically use.

The polymerase chain reaction (PCR) was used to amplify a fragment (approximately 400 base pairs) of the mitochondrial cytochrome *b* gene with the following universal primers described by Palumbi (1996): L14724 (5′-GTG ACT TGA AAA ACC ACC GTT G-3′) and Kocher et al. (1989): H15149 (5′-TGC AGC CCC TCA GAA TGA TAT TTG TCC TCA-3′). We chose this particular fragment for two reasons: 1) cytochrome *b* is commonly used in systematic studies of fishes and a wide variety of fish taxa are documented in the GenBank[1] data base, including percids (e.g., Song et al., 1998; Near, 2002; Sloss et al., 2004); and 2) our previous experience has shown that PCR amplification of smaller fragments is often more successful than amplification of larger fragments, especially when dealing with degraded samples such as extracts from deep-fried fillets.

The PCR mixture consisted of a total volume of 50 µL, with concentrations of 1.5 mM (milli Molar) $MgCl_2$, 1.0 µM (micro Molar) of each primer, and 1.0 U (units) of *Taq* polymerase. Amplification parameters consisted of an initial denaturation at 94°C for 2.5 min, followed by 35 cycles of denaturation (94°C, 1 min), primer annealing (52°C, 1 min), and polymerase extension (72°C, 1 min). A final extension at 72°C for 7 min was included to reduce the number of partial strands. Amplification products were then purified by running the entire product

[1] GenBank. 2006. National Center for Biotechnology Information (NCBI), National Institutes of Health, 8600 Rockville Pike, Bethesda, MD 20894. Website: http://www.ncbi.nlm.nih.gov (accessed 14 February 2006).

Manuscript submitted 16 June 2006 to the Scientific Editor's Office.

Manuscript approved for publication 6 September 2006 by the Scientific Editor.

Fish. Bull. 105:292–295 (2007).

on a 2% agarose gel in TAE (Tris-acetate-EDTA, p.H. 8.0) buffer. The band was made visible with ethidium bromide staining and was then excised and purified in a spin column. The resulting gel-purified PCR product was then used as a template for another round of PCR with identical parameters. Samples consisting of 250 ng (nanograms) of purified PCR product and 16 pmol (pico moles) of primer (L14724) were sequenced on an automated ABI 3700 sequencer (Applied Biosystems Inc., Fullerton, CA).

Because we did not know the identity of the species in the fish fillets, each sequence was submitted to a BLAST (basic local alignment search tool) search on the NCBI GenBank[1] database, which provides the identification of species by sequences. After we were confident that the identities of the species in the fillets were limited to the genus *Perca*, the sequences were aligned sequentially with cytochrome *b* sequence data from all three species of *Perca* (e.g., *P. flavescens*, *P. fluviatilis*, and *P. schrenkii*), and two outgroup percid taxa (walleye [*Sander vitreus*] and ruffe [*Gymnocephalus cernuus*]) by using the computer program CLUSTALX2[2] (Thompson et al., 1997). A tree of the relationships among the sequences was constructed by using maximum likelihood estimates of sequence divergences with a neighbor-joining network (Saitou and Nei, 1987) as implemented in the computer program PHYLIP (PHYLogeny Inference Package; Felsenstein[3]).

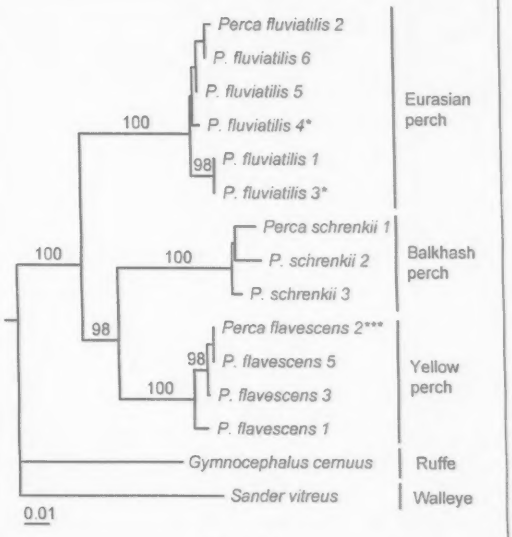


Figure 1

Phylogenetic relationships among *Perca* and outgroup mtDNA haplotypes as inferred from cytochrome *b* sequence divergences. Taxon labels are consistent with those in Table 1. * = sequence match to an individual fried fish fillet sample sequenced in this study. Numbers at nodes indicate percent support for the relationships from 1000 bootstrap pseudoreplications.

Results and discussion

Our extraction procedure yielded DNA usable for PCR and subsequent sequencing, although the extractions were degraded and of relatively low molecular weight. Thirteen complete cytochrome *b* sequences representing all three species of *Perca* were found documented on GenBank[1] (Table 1). Yellow perch is one of three described species of this genus, for which a substantial fishery exists in the Great Lakes, although fish stocks have declined at some localities.[4] The natural distribution of yellow perch extends from Nova Scotia south along the Atlantic coast of North America to South Carolina, and west to Montana (Scott and Crossman, 1973; Craig, 2000). The Eurasian perch is very similar morphologically to *P. flavescens*, is found throughout most of northern Europe and Asia (Craig, 2000; Maitland, 2000), and also represents a commercially important species. A third species, *P. schrenkii* Kessler, is restricted to the eastern portion of Kazakhistan and does not contribute to the world market.

Each species of *Perca* is represented by unique nucleotide cytochrome *b* sequences and has marked divergences (Fig. 1). Three of our five samples matched one of the cytochrome *b* sequences of the yellow perch *P. flavescens* (designated as *flavescens* 2), and two matched sequences of the Eurasian perch *P. fluviatilis* (denoted as *fluviatilis* 3 and *fluviatilis* 4). It is noteworthy that large genetic divergences separate the mtDNA cytochrome *b* sequences of *P. flavescens* and *P. fluviatilis*. These two species differ at 130 sites (11.4%; Song et al., 1998; Sloss et al., 2004), and intraspecific variation for each is an order of magnitude less (Fig. 1; also see Billington, 1993). Thus, it is unlikely that our identifications were in error.

Although one would expect that most of the perch fillets at local markets are caught locally, the supply of and demand for North American and Eurasian perch determines which species is the most economical to serve. Importers and exporters trade fish from both sides of the ocean and the price fluctuates seasonally for both species. Winter is the low supply period for both,

[2] Gibson, T., D. Higgins, J. Thompson, and F. Jeanmougin. 2006. ClustalX. Plate-forme de bio-informatique (Bioinformatic platform), I.G.B.M.C., 1 rue Laurent Fries, 67404 Illkirch, Cedex, France. Website: http://bips.u-strasbg.fr/fr/Documentation/ClustalX (accessed 14 February 2006).

[3] Felsenstein, J. 1995. Department of Genome Sciences, University of Washington, Box 357730, Seattle, Washington, USA 98195-7730. Website: http://evolution.genetics.washington.edu/phylip/general.html (accessed 20 February 2006).

[4] Johnson, T. B. 2006. Personal commun. Ontario Ministry of Natural Resources, Glenora Fisheries Station, R.R. #4, 21 Hatchery Lane, Picton, Ontario, Canada K0K 2T0.

Table 1

Taxonomic assignment and GenBank (Footnote 1 in the main text) accession numbers for each of the diagnostic mitochondrial cytochrome *b* sequences used in our comparisons with unknown fried fish fillets. Sequences from ruffe (*Gymnocephalus cernuus*) and walleye (*Sander vitreus*) were used for outgroup comparison. Taxonomic labels are consistent with the labeling on the tree in Figure 1. Each asterisk denotes that a single fried fish fillet sample was matched to this known sequence. * = one sample matched; *** = three samples matched.

Taxon	Haplotype designation	GenBank accession number
Yellow perch	*Perca flavescens* 1	AY374280
	P. flavescens 2***	AF546115
	P. flavescens 3	AF386600
	P. flavescens 4	AF045357
Eurasian perch	*Perca fluviatilis* 1	AY374281
	P. fluviatilis 2	AF546117
	P. fluviatilis 3*	AF546116
	P. fluviatilis 4*	AY929376
	P. fluviatilis 5	AF386599
	P. fluviatilis 6	AF045358
Balkash perch	*Perca schrenkii* 1	AF546120
	P. schrenkii 2	AF546119
	P. schrenkii 3	AF546118
Ruffe	*Gymnocephalus cernuus*	AF386598
Walleye	*Sander vitreus*	AF386602

but prices quickly fall as the ice clears from the Great Lakes.[4] In North America, the fishery in Lake Michigan (near Milwaukee, Wisconsin) crashed by 2000 and most perch taken in the past from the Great Lakes are presently taken from Lake Erie.[4,5,6]

Lake Erie itself is divided into four quota zones across both U.S. and Canadian waters, of which Zone 2 (comprising the west-central basins) has the largest U.S. allowable quota.[4,5,6] Most of those perch are landed and processed in Wheatley, Ontario, where the largest processing plants are located.[4,6] Current landed prices for North American yellow perch are about Can $2.00/lb, whereas the market price for processed fish runs about Can $8–9/lb.[4] Eurasian perch have been sold in North American markets for over 20 years, and presently are cheaper than North American yellow perch, selling for Can $2–3/lb.[4] Thus, restaurants in the Great Lakes area that advertise yellow perch "fish fries" may be unlikely to offer economical all-you-can-eat dinners and stay in business without imported Eurasian perch. Our results illustrate that use of mtDNA sequencing is an economic and effective method to identify the species in fillets for perch (and other species), even in the case of genetic material that has been deep fried.

[5] Baldwin, N. S., R. W. Saalfeld, M. R. Dochoda, H. J. Buettner, and R. L. Eshenroder. 2002. Commercial Fish Production in the Great Lakes 1867–2000. Website: http://www.glfc.org/databases/commercial/commerc.php (accessed on 26 July 2006).

[6] Bader, T. J. 2005. Personal commun. Ohio Division of Wildlife, Fairport Fish Research Unit, 1190 High St., Fairport Harbor, OH, USA 44077.

Acknowledgments

We thank T. Johnson (Ontario Ministry of Natural Resources) and T. Bader (Ohio Division of Wildlife) for information regarding the Lake Erie perch fishery and the importation of Eurasian yellow perch. We also thank R. Knight (Ohio Division of Wildlife) for providing valuable comments on the manuscript, along with Great Lakes Genetic Laboratory graduate students A. Haponski and M. Neilson and research technician R. Lohner for help. This study was supported by grants to C. Stepien from the Lake Erie Protection Fund no. 00-15, NOAA Sea Grant no. R/LR-7 through Ohio Sea Grant, and USEPA CR-83281401-0. RMS was supported as a postdoctoral researcher in the Great Lakes Genetics Laboratory. This is contribution number 2007-04 from the Lake Erie Center.

Literature cited

Billington, N.
1993. Genetic variation in Lake Erie yellow perch (*Perca flavescens*) demonstrated by mitochondrial DNA analysis. J. Fish Biol. 43:941–943.

Craig, J. F.
2000. Percid fishes: systematics, ecology, and exploitation, 352 p. Blackwell Science, Oxford, UK.

Faber, J. E., and C. A. Stepien.
1997. The utility of mitochondrial DNA control region sequences for analyzing phylogenetic relationships among populations, species, and genera of the Percidae. *In* Molecular systematics of fishes (T. D. Kocher, and C. A. Stepien, eds.), p. 129–134. Academic Press, San Diego, CA.

Ford, A. M., and C. A. Stepien.
2004. Genetic variation and spawning population structure in Lake Erie yellow perch, *Perca flavescens*: a comparison with a Maine population. *In* Proceedings of Percis III, the 3rd international symposium on percid fishes (T. P. Barry, and J. A. Malison, eds.), p. 131–132. Univ. Wisconsin Sea Grant Institute, Madison, WI.

Kocher, T. D., W. K. Thomas, A. Meyer, S. V. Edwards, S. Paabo, F. X. Villablanca, and A. C. Wilson.
1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Natl. Acad. Sci. USA 86:6196–6200.

Maitland, P. S.
2000. Guide to freshwater fish of Britain and Europe, 256 p. Octopus Publ. Group, Ltd., London, UK.

Near, T. J.
2002. Phylogenetic relationships of *Percina* (Percidae: Etheostomatinae). Copeia 2002:1–14.

Palumbi, S. R.
1996. Nucleic acids II: The polymerase chain reaction. *In* Molecular systematics, 2nd ed. (D. M. Hillis, C. Moritz, and B. K. Mable, eds.), p. 205–247. Sinauer Assoc., Sunderland, MA.

Saitou, N., and M. Nei.
1987. The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol. Biol. Evol. 4:406–425.

Scott, W. B., and E. J. Crossman.
1973. Freshwater fishes of Canada, 966 p. Fish. Res. Board Can., Ottawa, Canada.

Sloss, B. L., N. Billington, and B. M. Burr.
2004. A molecular phylogeny of the Percidae (Teleostei, Perciformes) based on mitochondrial DNA sequence. Mol. Phylogenet. Evol. 32:545–562.

Song, C. B., T. J. Near, and L. M. Page.
1998. Phylogenetic relations among percid fishes as inferred from mitochondrial cytochrome *b* DNA sequence data. Mol. Phylogenet. Evol. 10:343–353.

Thompson, J. D., T. J. Gibson, F. Plewnial, F. Jeanmougin, and D.G. Higgins.
1997. The CLUSTALX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Res. 22:4673–4680.

Ward. R. D.
2000. Genetics in fisheries management. Hydrobiologia 420:191–201.

Natural mortality rate, annual fecundity, and maturity at length for Greenland halibut (*Reinhardtius hippoglossoides*) from the northeastern Pacific Ocean

Daniel W. Cooper (contact author)[1]
Katherine P. Maslenikov[2]
Donald R. Gunderson[2]

Email address (for D. W. Cooper): dan.cooper@noaa.gov

[1] Alaska Fisheries Science Center F/AKC 2
7600 Sand Point Way NE
Seattle, Washington 98115-0700.

[2] University of Washington
School of Aquatic and Fishery Sciences
1122 NE Boat Street
Seattle, Washington 98195.

Mortality, fecundity, and size at maturity are important life history traits, and their interactions determine the evolution of life history strategies (Roff, 1992; Stearns, 1992; Charnov, 2002). These same traits are also important for population dynamics models (Hunter et al., 1992; Clark, 1999). It is increasingly important to accurately determine Greenland halibut (*Reinhardtius hippoglossoides*) life history traits and to correctly assess the status of its stocks because low recruitment or low biomass estimates have led to catch restrictions in the Bering Sea and Aleutian Islands (Ianelli et al.[1]), the Northeastern Arctic (Ådlandsvik et al., 2004), and the Northwest Atlantic (Bowering and Nedreaas, 2000).

Mortality has been estimated for stocks of Greenland halibut from the Northwest Atlantic (Bowering, 1983) and from the Bering Sea (Ianelli et al.[1]) from population age structures where a maximum age near 20 years has been assumed. However, recent age validation (Treble et. al[2]) and a new aging technique (Gregg et al., 2006) indicate that Greenland halibut may have a lower mortality rate and live longer. Fecundity estimates (Gundersen et al., 2000) and length at maturity estimates (Morgan et al., 2003) vary by geographic area and year for Greenland halibut in the Atlantic. Fecundity of Greenland halibut from the Bering Sea has been estimated once (D'yakov, 1982), and no estimates for Greenland halibut maturity at length have been reported from Alaskan waters.

A significant and positive relationship between natural mortality rate (M) and annual reproductive effort, as measured by gonadosomatic index (GSI=*ovary weight/somatic body weight*), was found for 28 fish stocks of a variety of species ($M=1.79\times GSI$, $r^2=0.75$) (Gunderson, 1997). This GSI-M relationship can provide an estimate of M independent of age data, and is desirable for Greenland halibut because age data are still controversial for this species. The objectives of this study are to estimate annual fecundity, length at 50% maturity, and the rate of instantaneous natural mortality (M) by using GSI for Greenland halibut from the Bering Sea and Aleutian Islands.

Materials and methods

Ovaries were collected by fishery observers and scientists from the National Marine Fisheries Service (NMFS) in the Bering Sea and Aleutian Islands (Table 1, Fig. 1). Fork length (cm) and somatic weight (kg) (ovaries and stomach contents removed) were recorded at sea. Total weight was approximated by adding somatic weight and the estimated fresh ovary weight.

Ovaries were removed and placed in a 10% formalin solution buffered with sodium bicarbonate. Twenty-eight ovaries were weighed (±2 g) before being placed in formalin. The fresh weight was later compared to formalin weight to determine a conversion factor when fresh weight was not available. Ovaries were removed from the 10% buffered formalin, blotted dry, and weighed (±0.001 g). When possible, a whole cross section was removed from one lobe of an ovary for histological analysis. If the ovary cross section was too large to fit on a slide, a wedge-shaped sample was removed which included tissue from the center of the ovary to the ovarian wall. Ovary tissue samples were embedded in paraffin, sectioned at 4 μm, and stained with hematoxylin and eosin. All 56 specimens smaller than 40 cm were obviously immature because of their very small ovaries; therefore histological examination was completed on only six of these specimens to verify that they were immature.

[1] Ianelli, J. N., T. K. Wilderbuer, and D. Nichol. 2005. Stock assessment and fishery evaluation: Bering Sea and Aleutian Islands Greenland turbot. Website: http:www.afsc.noaa.gov/refm/docs/2005/BSAIGturbot.pdf (accessed on 28 June 2006).

[2] Treble, M. A., S. E. Campana, R. J. Wastle, C. M. Jones, and J. Boje. 2005. An assessment of age determination methods, with age validation of Greenland halibut from the Northwest Atlantic. NAFO SCR Doc. 05/43, 22 p. Northwest Atlantic Fisheries Organization, P.O Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

Manuscript submitted 18 March 2005 to the Scientific Editor's Office.
Manuscript approved for publication 8 September 2006 by the Scientific Editor.
Fish. Bull. 105:296–304 (2007).

Each slide was analyzed for the oocyte stages present and for postovulatory follicles (POFs) according to the descriptions and images from Gundersen (2003) (Fig. 2). Maturity stages were assigned according to Gundersen et al. (2003).

Length-GSI relationship and instantaneous rate of natural mortality

For the GSI-M relationship, Gunderson (1997) defined GSI as the point in ovarian development when the ovaries had attained maximum weight due to vitellogenesis, but had not gained nonenergetic weight (due to hydration). For this study, fish with ovaries in maturity stage vitellogenesis 4 (Fig. 2) were used in the GSI-M estimate. Fish with ovaries containing hydrated oocytes or POFs were excluded. Fedorov (1968) found that dry weights of oocytes corresponding to the vitellogenesis-4 stage (yolk-filled oocyte in the trophoplasmic growth stage) were equal to dry weights of hydrated ova; this result indicates that yolk deposition is completed at the vitellogenesis-4 stage.

The length of the average mature female in an unexploited population is required for Gunderson's (1997) GSI-M relationship. The foreign trawl fishery prior to 1988 showed the best selectivity for fish in the widest size range (Ianelli and Wilderbuer[3]). Foreign trawl fishery data from the NMFS Observer program (Berger[4]) were analyzed, and the oldest complete data set (1977–87) was chosen to best approximate the true nature of the Greenland halibut population in the absence of fishing pressure. The mean length of mature females was determined from the weighted length by using data on the abundance at each length as weights.

Potential annual fecundity

To test for homogeneity of vitellogenic oocyte density throughout the ovaries, subsamples were selected from nine fish at three locations (anterior, middle, and posterior) on each ovary lobe (eyed side and blind side) for a total of six subsamples per fish. Cross sections were taken through the ovary and included the ovarian wall. For the anterior and middle sections, one half of the cross section was used as the subsample. The posterior cross sections of the ovary were much smaller and therefore the entire cross section was used. The subsamples had a mean weight of 2.07 grams (standard error [SE]=0.14) and a mean number of 553 vitellogenic oocytes (SE=43.11). Oocyte density (number of oocytes/gram of ovarian tissue) and diameters of 50 of the most advanced oocytes per fish were recorded.

Two-way ANOVAs were used to test for differences in oocyte density and diameter between ovarian lobes and among ovarian locations. Paired *t*-tests were used to identify differences among ovarian locations when the ANOVA detected significant differences.

Greenland halibut are reported to have determinate fecundity (Gundersen et al., 2001; Junquera et al.,

Figure 1

Map of locations where Greenland halibut (*Reinhardtius hippoglossoides*) were collected for ovary samples. Open circles mark locations where fish were collected for the ovary samples. Filled circles mark locations where fish were collected for the natural mortality (*M*) estimate.

Table 1

Number of Greenland halibut (*Reinhardtius hippoglossoides*) females collected by month and year.

	Year					
Month	1999	2000	2002	2003	2004	Total
January						
February						
March					19	19
April						
May						
June		13	3	1		17
July		44	8	101		153
August						
September	78	42				120
October		2				2
November						
December						
Total	78	101	11	102	19	311

[3] Ianelli, J. N., and K. T. Wilderbuer. 1995. Greenland turbot (*Reinhardtius hippoglossoides*) stock assessment and management in the Eastern Bering Sea. *In* Proceedings of the International Symposium on North Pacific flatfish, p. 407–441. Alaska Sea Grant report 95-04. Univ. Alaska Sea Grant College Program, P. O. Box 755040, Fairbanks, AK 99775.

[4] Berger, J. 2002. Personal commun. Alaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115.

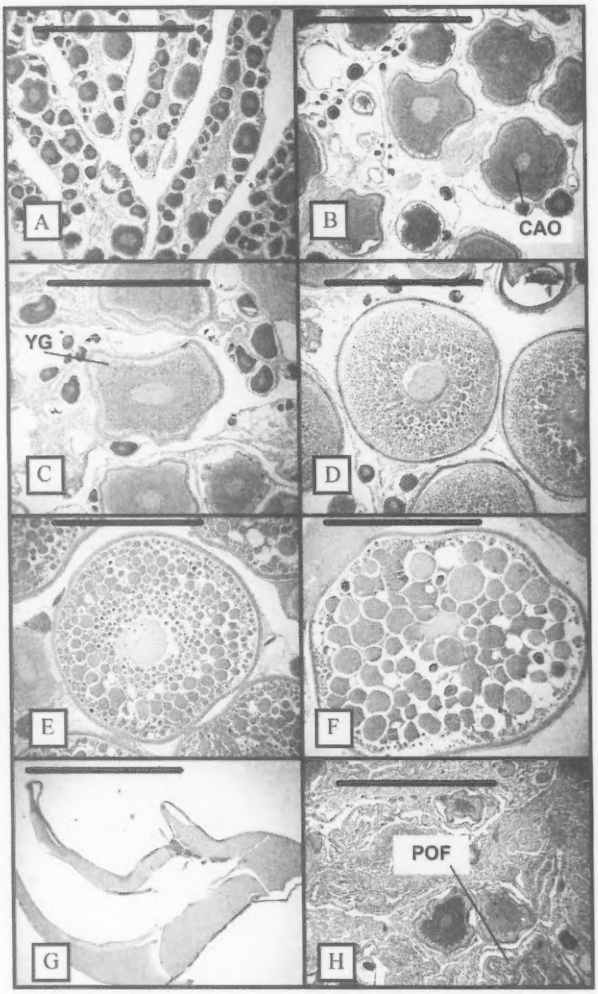


Figure 2

Ovary stages of Greenland halibut (*Reinhardtius hippoglossoides*) from histology. Ovary staging follows the methods of Gundersen (2003). All scale bars = 1.0 mm. (**A**) Immature. (**B**) Cortical alveoli. CAO = cortical alveolar oocyte. (**C**) Vitellogenesis 1. YG = yolk globules. (**D**) Vitellogenesis 2. Note the largest yolk globules are located near the nucleus. (**E**) Vitellogenesis 3. Note the yolk size gradient has been reversed and the largest yolk globules are near the periphery of the oocyte. (**F**) Vitellogenesis 4. The yolk globules are all large and have begun to fuse. (**G**) Spawning. (**H**) Spent. POF = postovulatory follicle.

2003). To confirm this for Greenland halibut in the Bering Sea, oocyte diameters were measured to determine if there is a hiatus in size between developing and reserve oocytes. Mean diameters of nonvitellogenic and vitellogenic oocytes were measured from whole oocyte tissue samples. All vitellogenic oocytes in a tissue sample of known weight were counted. The oocytes were placed in a dish on top of a sampling grid. All

oocytes touching the lines of the sampling grid were measured until 50 nonvitellogenic and 50 vitellogenic oocytes had been measured. Nonvitellogenic oocytes were reported as percent frequency, whereas vitellogenic oocytes were reported as number of vitellogenic oocytes per gram of ovary tissue. Because oocyte diameter may vary by ovary location (see "Results" section), all oocyte measurements were taken from the middle location of the ovaries.

To select ovaries suitable for fecundity estimates, the diameters of six vitellogenic oocytes sectioned through the nucleus were measured from the histological sections by using a microscopic image analysis system. Because oocytes were not perfectly round, oocyte diameter was calculated from oocyte area with the following equation:

$$Diameter = 2\sqrt{\frac{Oocyte\ Area}{\pi}}.$$

Females with the mean diameter of vitellogenic oocytes smaller than 1000 µm were excluded from the fecundity estimate because not all oocytes to be spawned in the current year could be identified (see "Results" section). To exclude fish that had already begun spawning, samples containing POFs or ova were excluded.

Fecundity was estimated gravimetrically by counting vitellogenic oocytes from weighed subsamples of ovarian tissue. The weight of the thick ovarian wall could not be discounted; therefore subsamples were cut with a proportionately weighted piece of ovarian wall attached. This procedure was accomplished by using either an entire cross section of the ovary, or a wedge-shaped sample cut from an entire cross section. Because small oocyte density differences were found between the posterior location and the anterior+middle locations, and between the eyed and blind lobes (see "Results" section), four subsamples were taken for each fish. The posterior region of each lobe and the area between the middle and anterior locations of each lobe were sampled. Weighting factors for the posterior and for the middle and anterior locations of the ovary were determined by calculating the proportional mass of these locations of the ovaries for 26 fish. The average proportional mass for the posterior and for the middle and anterior locations was 0.11 and 0.89 (SE: 0.0048), respectively. When divided by two (to account for the two ovary lobes), the average weighting factors for the posterior blind and eyed lobes = 0.06, and the average weighting factor of the anterior and middle locations for the blind and eyed lobes = 0.44. Fecundity of each female was estimated from the four subsamples by using the fecundity equation with weighting factors from Nichol and Acuna (2001) to account for the smaller proportional mass of the posterior sections.

The fraction of vitellogenic oocytes undergoing atresia was estimated for 174 fish from histological cross sections. The total number of vitellogenic oocytes and the number of atretic vitellogenic oocytes (Hunter and Macewicz, 1985) for each histological section were counted. The fraction of vitellogenic oocytes undergoing atresia was estimated as the number of atretic vitellogenic oocytes divided by the total number of vitellogenic oocytes.

Length at maturity

Maturity was determined histologically, by using all fish 40 cm and larger, and a subsample (n=6) of females less than 40 cm. Maturity stages were determined according to the method of Gundersen (2003).

Results

Length-GSI relationship and instantaneous rate of natural mortality

The conversion factor between ovary fresh weight and weight after fixation and storage in formalin was:

$$Fresh = (1.437 \times Formalin) + 6.8276, \quad (n=28,\ r^2=0.9903),$$

where *Fresh* = fresh ovary weight (g); and
Formalin = ovary weight after storage in formalin (g).

Maturity stages increased from spring (March) to summer (June and July) and again to autumn (September and October) (Fig. 3). In March, mature females were spawning, spent, or beginning vitellogenesis for the next spawning season. Most fish were in the vitellogenesis-1 stage. By June–July, the ovaries had advanced until most were in the vitellogenesis-2 stage, although some were also in stages vitellogenesis 1 and 3. By September–October, the majority of mature ovaries were in vitellogenesis-3 stage, although some had progressed to vitellogenesis 4 and a small percentage (4%) of the mature females collected in September were ready to spawn (presence of hydrated oocytes) or showed signs of recent spawning (presence of ova or POFs). The largest mean oocyte diameter (n=6 for histological examination) for any female with oocytes before hydration was 1720 µm.

The mean length of mature females was 79.2 cm during 1977–87, and the GSI data were derived from females smaller and greater than 79.2 cm. The GSI was very poorly correlated with length (r^2=0.04), and we used the mean GSI (0.063, σ^2=0.000018) in our sample to obtain a natural mortality estimate of M = 0.112. The variance of M ($Var\,\hat{M}$, 0.0002) was estimated according to the method of Gunderson et al. (2003) with the following equation:

$$Var\hat{M} = (\overline{GSI})^2 Var(\hat{k}) + \hat{k}^2 Var(\overline{GSI}),$$

where $Var\,\hat{M}$ = the variance of mortality;
$\overline{GSI}$ = mean value of GSI; and
$\hat{k}$ = constant from the GSI-M regression (Gunderson, 1997).

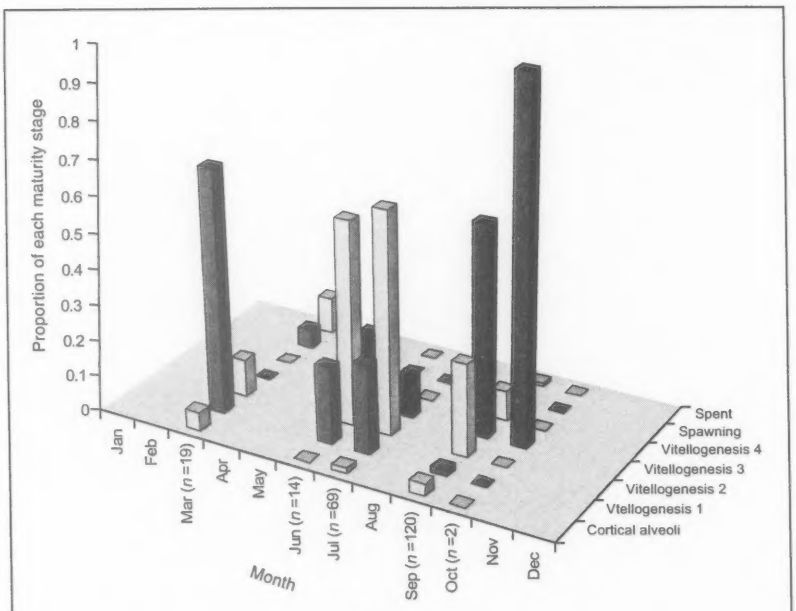


Figure 3

Proportion of Greenland halibut (*Reinhardtius hippoglossoides*) females in each histological maturity stage by month. The number of females (n) is noted for each month along the x-axis. Ovaries were collected in March 2004; June 2000, 2002, 2003; July 2000, 2002, 2003; September 1999, 2000; and October 2000.

The final estimate of instantaneous natural mortality (M) in our study had a standard error of 0.0138, yielding a 95% confidence interval of 0.08–0.14).

Potential annual fecundity

When nine females were tested for the difference in mean oocyte density by ovary location, the difference was significant (two-way ANOVA, $P<0.01$, df=2 , $F=19.7$). Mean oocyte densities were 280, 276, and 240 in the anterior, middle, and posterior locations in ovaries, respectively. Paired t-tests indicated that the posterior location had a significantly lower oocyte density than middle ($P<0.001$) or anterior locations ($P<0.001$), whereas the middle and anterior locations were not significantly different from each other ($P=0.19$). Oocyte density was also slightly lower in the eyed (259 eggs/gram) than in the blind lobe (272 eggs/gram; two-way ANOVA, $P=0.034$, df=1, $F=4.8$).

Mean oocyte diameters also varied significantly by ovary location (two-way ANOVA, $P=0.047$, df=2, $F=3.4$). Mean oocyte diameters for the anterior, middle, and posterior locations were 1611, 1627, and 1609 μm, respectively. We observed two distinct and separate oocyte size-frequency modes corresponding to nonvitellogenic and vitellogenic oocytes when the average vitellogenic oocyte diameter exceeded 1000 μm (Fig.4). On the basis of these results, we decided to include only those samples where the mean vitellogenic oocyte diameter was greater than 1000 μm ($n=6$ oocytes per specimen for histological examination).

Potential annual fecundity data conformed more closely to a linear regression on total weight:

$$Fec = 13.438\ (Wt_{total}(g)) - 436.4438 \quad r^2=0.6206,\ n=47$$

where Fec = fecundity; and
Wt_{total} = total weight,

than to a nonlinear regression on length (Fig. 5):

$$Fec = 0.0266\ (ForkLength(\text{cm}))^{3.3654}, \quad r^2=0.4969,\ n=47$$

where Fec = fecundity; and
$ForkLength$ = fork length.

The highest fractions of atretic vitellogenic oocytes occurred in females with oocytes in early stages of vitellogenesis. Once the largest cohort of vitellogenic oocytes reached a diameter of 750 μm, the fraction of atresia was greater than 0.20 for only one of 153 specimens. Over 77% of females with developing oocytes had fractions of atresia of 0.05 or less, and over 90% of females had fractions of atresia of 0.10 or less. For fish that met oocyte diameter criteria for fecundity estimates

Table 2

Greenland halibut (*Reinhardtius hippoglossoides*) female length (cm) at 50% maturity determined in the present study and in other studies. Examination method column indicates whether visual macroscopic gonad inspection or histological examination was used to assign maturity stages.

Study	Examination method	Area	Length
This study	Histological	Bering Sea, Aleutian Islands	65–70
Walsh and Bowering (1981)	Histological and visual	Northern Labrador	75–80
Nielsen and Boje[1]	Histological	West Greenland Fjords	65
Junquera et al. (1999)	Visual, checked with histological	Flemish Cap (N. Atlantic)	64.5–69.5
Gundersen (2003)	Visual, checked with histological	Barents Sea	57.8
Morgan et al. (2003)	Visual	Gulf of St. Lawrence 1978–1981	58.2
Morgan et al. (2003)	Visual	Gulf of St Lawrence 1996–2000	48.2
Morgan et al. (2003)	Visual	Labrador-eastern Newfoundland	78.5
Morgan et al. (2003)	Visual	Eastern Greenland	62.7
Morgan et al. (2003)	Visual	Iceland	64
Morgan et al. (2003)	Visual	Barents Sea (Norwegian data)	57.3
Morgan et al. (2003)	Visual	Barents Sea (Russian data)	60.6

[1] Nielsen, J. G., and J. Boje. 1995. Sexual maturity of Greenland halibut at West Greenland based on visual and histological observations. NAFO SCR Doc. 95/18, 7 p. Northwest Atlantic Fisheries Organization, P.O Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

(mean diameter of vitellogenic oocytes >1000 μm), the mean fraction of atretic vitellogenic oocytes was 0.04 (standard deviation [SD]=0.05, n=108).

Length at maturity

All females smaller than 65 cm were categorized as immature, although few females were collected between 51 and 60 cm (2 females between 61 and 65 cm, and 4 females between 56 and 60 cm). All females larger than 70 cm were categorized as mature.

Discussion

Maturity at length

No precise estimate of female length at 50% maturity was possible because of a scarcity of collected samples near the presumed length at 50% maturity. The data indicate length at 50% maturity is somewhere between 65 and 70 cm and is higher than the 60 cm value currently used in stock assessment (Ianelli et al.[1]). Estimates for female length at 50% maturity for this species in other geographic regions range from 48–80 cm (Table 2).

Fecundity

Atresia followed the same general pattern as reported by Gundersen (2003) and did not have a large effect on annual fecundity. Fecundity at length from our study was somewhat higher than that reported by D'yakov (1982) from samples collected in 1978 in the Bering Sea. The results from both our study and D'yakov's study (1982) fall within reported ranges of fecundity from other regions; however there is strong variation between the regions in fecundity at length (Fig. 5). Gundersen (2003) hypothesized a geographic variation in fecundity for Greenland halibut. This variation may be caused by a trade-off between egg size and fecundity (Roff, 1992). The largest vitellogenic oocytes before hydration in our study were about 1700 μm, compared to 2800 μm reported by Gundersen (2003) for samples collected in the Barents Sea. Fecundity estimates by Gundersen (2000) from samples collected in the Barents Sea in 1996, 1997, and 1998 were all lower than the fecundity estimates from our study (Fig. 5).

Length-GSI relationship and instantaneous rate of natural mortality

The estimated rate of instantaneous natural mortality of 0.112 from our study is lower than the value of M currently used in the Bering Sea and Aleutian Islands stock assessment. The stock assessment uses a maximum age of 21 to estimate M to be 0.18 (Ianelli et al.[1]).

Our estimate for M corresponds more closely with results from Gregg et al. (2006) who aged Greenland halibut from the Bering Sea up to 36 years, corresponding to an M of 0.115. A recent age validation study has revealed that Greenland halibut in the Atlantic live up to 33 years, which is also older than previous estimates (Treble et al.[2]). Overestimating M may result in unsustainably high target harvest rates (Clark, 1999).

This study provides a length range for estimated length at 50% maturity, annual fecundity, and an

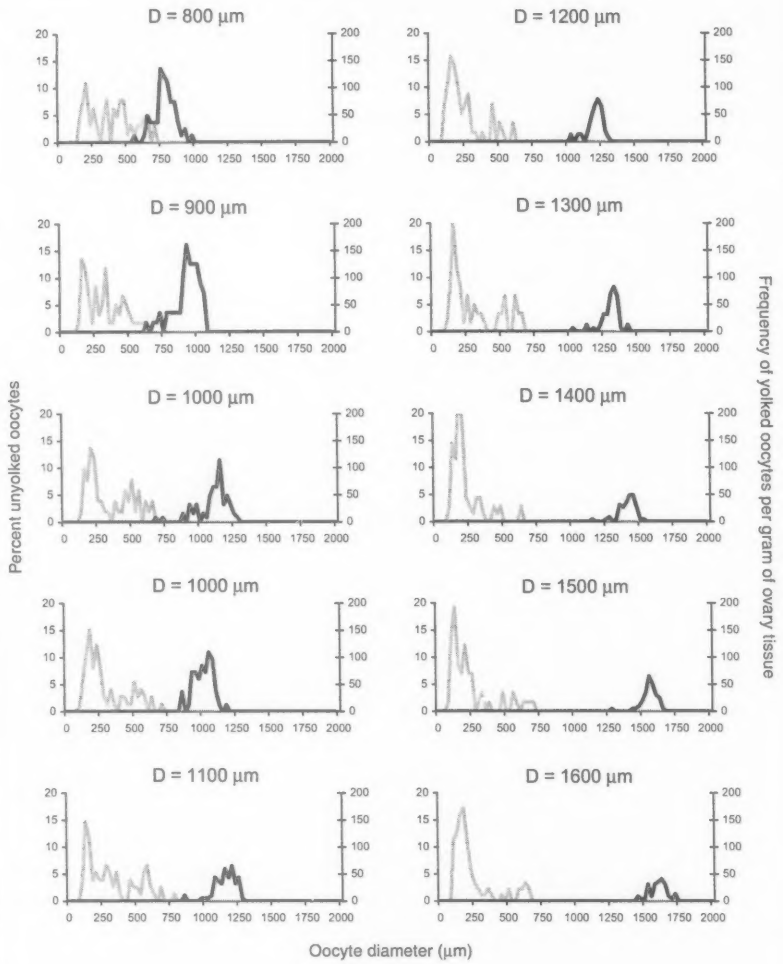

D = 800 µm
D = 1200 µm
D = 900 µm
D = 1300 µm
D = 1000 µm
D = 1400 µm
D = 1000 µm
D = 1500 µm
D = 1100 µm
D = 1600 µm
Percent unyolked oocytes
Frequency of yolked oocytes per gram of ovary tissue
Oocyte diameter (µm)

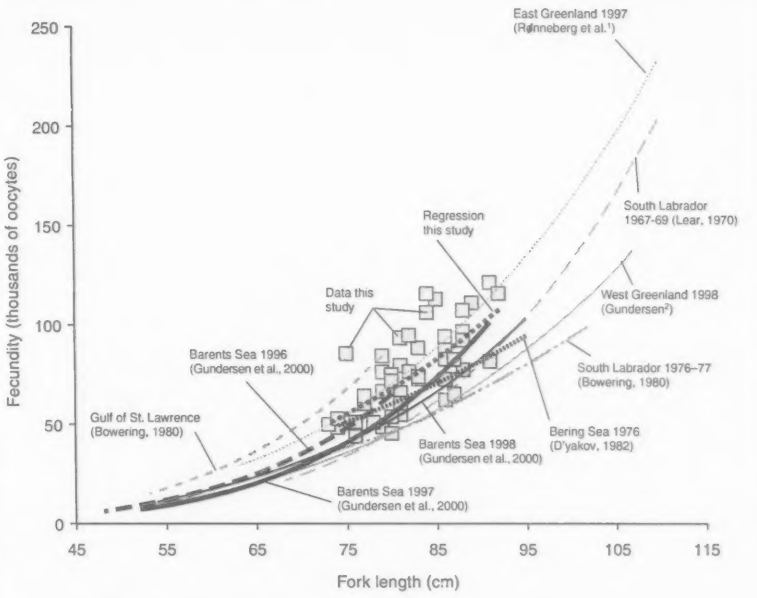
Figure 4

Frequency of oocyte diameter for 10 female Greenland halibut (*Reinhardtius hippoglossoides*) arranged in progression of vitellogenic oocyte mean diameter (D). Data for non-vitellogenic oocytes (in gray) are plotted in terms of percent frequency, and vitellogenic oocytes (in black) in terms of number of oocytes per gram of ovary tissue.

estimate of instantaneous natural mortality independent of age data for a species with an uncertain age structure. Fecundity was higher and eggs were smaller in Greenland halibut from Alaskan waters than the reported values for the Barents Sea. This may be due to a trade-off between number of eggs and egg size (Roff, 1992). Based on the energy invested in annual reproduction (GSI), Greenland halibut mortality (M) appears lower than the values used currently in population models.

Acknowledgments

We thank the scientists of Resource Assessment and Conservation Engineering division of the Alaska Fishery Science Center, and the following fishery observers for ovary collections: J. Bennett, K. Fleming, R. Hutson, C. Hilderbrandt, N. Goddard, A. Randi, and S. Rothamel. D. Kimura, S. McDermott, and D. Nichol provided valuable comments on manuscript drafts. This publication was funded by the Joint Institute for the Study



[1] Rønneberg, J. E., A. C. Gundersen, and J. Boje. 1998. Fecundity of Greenland halibut (*Reinhardtius hippoglossoides*) in East Greenland waters, July 1997. ICES C. M. (Council Meeting) 1998/0:26, 12 p.

[2] Gundersen, A. C. 2002. Note on fecundity of Greenland halibut in West Greenland waters. *In* Reproduction of West-Nordic Greenland halibut (A. C. Gundersen, ed.) p. 197–210. TEMA NORD 2002: 519, Nordic Council of Ministers, Store Strandstraend 18, DK-1255 Copenhagen, Denmark.

Figure 5

Greenland halibut (*Reinhardtius hippoglossoides*) fecundity-at-length data and fitted regression lines for this (n=47, r^2=0.50) and other studies.

of the Atmosphere and Ocean (JISAO) under NOAA Cooperative Agreement no. NA17RJ1232, contribution no. 1088.

Literature cited

Ådlandsvik, B., A. C. Gundersen, K. H. Nedreaas, A. Stene, and O. L. Albert.
2004. Modeling the advection and diffusion of eggs and larvae of Greenland halibut (*Reinhardtius hippoglossoides*) in the north-east Arctic. Fish. Oceanogr. 13:403–415.

Bowering, W. R.
1980. Fecundity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), from Southern Labrador and Southeastern Gulf of St. Lawrence. J. Northwest Atl. Fish. Sci. 1:39–43.
1983. Age, growth, and sexual maturity of Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the Canadian Northwest Atlantic. Fish. Bull. 81:599–611.

Bowering, W. R., and K. H. Nedreaas.
2000. A comparison of Greenland halibut (*Reinhardtius hippoglossoides* (Walbaum) fisheries and distribution in the Northwest and Northeast Atlantic. Sarsia 85:61–76.

Charnov, E. L.
2002. Reproductive effort, offspring size, and benefit/cost ratios in the classification of life histories. Evol. Ecol. Res. 4:749–758.

Clark, W. G.
1999. Effects of an erroneous natural mortality rate on a simple age-structured stock assessment. Can. J. Fish. Aquat. Sci. 56:1721–1731.

D'yakov, Y. P.
1982. The fecundity of the Greenland halibut, *Reinhardtius hippoglossoides* (Pleuronectidae), from the Bering Sea. J. Ichthyol. 22(5):59–64.

Fedorov, K. Y.
1968. Oogenesis and the sexual cycle of the Greenland halibut. [In Russian]. Tr. Palyarn. Nauchno-Issled. Proektn. Inst. Morsk. Rybn. Khoz Okeanogr. 23:425–450.

Gregg, J. L., D. M. Anderl, and D. K. Kimura.
2006. Improving the precision of otolith-based age estimates for Greenland halibut (*Reinhardtius hippoglossoides*) with preparation methods adapted for fragile sagittae. Fish. Bull. 104:643–648.

Gundersen, A. C.
2003. Sexual maturity, fecundity and nursery grounds of Northeast Arctic Greenland halibut (*Reinhardtius*

hippoglossoides (Walbaum). Ph. D. diss., 166 p. Univ. Bergen, Bergen, Norway.

Gundersen, A. C., K. H. Nedreaas, O. S. Kjesbu, and O. T. Albert.
2000. Fecundity and recruitment variability of Northeast Arctic Greenland halibut during 1980–1998, with emphasis on 1996–1998. J. Sea Res. 44:45–54.

Gundersen, A. C., J. E. Ronnegerg, and J. Boje.
2001. Fecundity of Greenland halibut (*Reinhardtius hippoglossoides* Walbaum) in East Greenland waters. Fish. Res. 51:229–236.

Gunderson, D. R.
1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. Can. J. Fish. Aquat. Sci. 54:990–998.

Gunderson, D. R., M. Zimmermann, D. G. Nichol, and K. Pearson.
2003. Indirect estimates of natural mortality rate for arrowtooth flounder and darkblotched rockfish. Fish. Bull. 101:175–182.

Hunter, J. R., and B. J. Macewicz.
1985. Rates of atresia in the ovary of captive and wild northern anchovy, *Engraulis mordax*. Fish. Bull. 83:119–136.

Hunter, J. R., B. J. Macewicz, N. C. Lo, and C. A. Kimbrell.
1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. 90:101–128.

Junquera, S., E. Roman, J. Morgan, M. Sainza, and G. Ramilo.
2003. Time scale of ovarian maturation in Greenland halibut (*Reinhardtius hippoglossoides*, Walbaum). ICES J. Mar. Sci. 60:767–773.

Junquera, S., E. Roman, X. Paz, and G. Ramilo.
1999. Changes in Greenland halibut growth, condition, and fecundity in the Northeast Atlantic (Flemish Pass, Flemish Cap and Southern Grand Bank). J. Northwest Atl. Fish. Sci. 25:17–28.

Lear, W.A.
1970. Fecundity of Greenland halibut (*Reinhardtius hippoglossoides*) in the Newfoundland-Labrador area. Fish. Res. Board Can. 27:1880–1882.

Morgan, M. J., W. R. Bowering, A. C. Gundersen, A. Hoines, B. Morin, O. Smirnov, and E. Hjorleifsson.
2003. A comparison of the maturation of Greenland Halibut (*Reinhardtius hippoglossoides*) from populations throughout the North Atlantic. J. Northwest Atl. Fish. Sci. 31:99–112.

Nichol, D. G., and E. I. Acuna.
2001. Annual and batch fecundities of yellowfin sole, *Limanda aspera*, in the eastern Bering Sea. Fish. Bull. 99:108–122.

Roff, D. A.
1992. The evolution of life histories: theory and analysis, 535 p. Chapman and Hall, New York, NY.

Stearns, S. C.
1992. The evolution of life histories, 249 p. Oxford Univ. Press, New York, NY.

Walsh, S. J., and W. R. Bowering.
1981. Histological and visual observations on oogenesis and sexual maturity in Greenland halibut off Northern Labrador. NAFO (North Atlantic Fisheries Organization) Sci. Counc. Stud. 1:71–75.

Validation of back-calculation equations for juvenile bluefish (*Pomatomus saltatrix*) with the use of tetracycline-marked otoliths

Marja E. Roemer

Department of Biology
University of Massachusetts Dartmouth
North Dartmouth, Massachusetts 02747

Kenneth Oliveira (contact author)

Department of Biology
University of Massachusetts Dartmouth
285 Old Westport Road
North Dartmouth, Massachusetts 02747

E-mail address for K. Oliveira: Koliveira@umassd.edu

In recent years, a decrease in the abundance of bluefish (*Pomatomus saltatrix*) has been observed (Fahay et al., 1999; Munch and Conover, 2000) that has led to increased interest in a better understanding the life history of the species. Estimates of several young-of-the-year (YOY) life history characteristics, including the importance and use of estuaries as nursery habitat (Kendall and Walford, 1979) and size-dependant mortality (Hare and Cowen, 1997), are reliant upon the accuracy of growth determination. By using otoliths, it is possible to use back-calculation formulae (BCFs) to estimate the length at certain ages and stages of development for many species of fishes. Use of otoliths to estimate growth in this way can provide the same information as long-term laboratory experiments and tagging studies without the time and expense of rearing or recapturing fish. The difficulty in using otoliths in this way lies in validating that 1) there is constancy in the periodicity of the increment formation, and 2) there is no uncoupling of the relationship between somatic and otolith growth.

To date there are no validation studies demonstrating the relationship between otolith growth and somatic growth for bluefish. Daily increment formation in otoliths has been documented for larval (Hare and Cowen, 1994) and juvenile bluefish (Nyman and Conover, 1988). Hare and Cowen (1995) found age-independent variability in the ratio of otolith size to body length in early age bluefish, although these differences varied between ontogenetic stages. Furthermore, there have been no studies where an evaluation of back-calculation methods has been combined with a validation of otolith-derived lengths for juvenile bluefish.

This study uses tetracycline-marked YOY bluefish otoliths to achieve two objectives: 1) to validate the relationship between somatic and otolith growth for juvenile bluefish, and 2) to compare the effectiveness of the Dahl-Lea equation, Fraser-Lee equation, scale proportional hypothesis (SPH), and body proportional hypothesis (BPH) length back-calculation formulae.

Materials and methods

Young-of-the-year bluefish were collected by beach seine (15 m × 1.2 m × 6 mm mesh) from Clarks Cove in Buzzards Bay, Massachusetts, in July and August 2005. The fish were anesthetized with eugenol (clove oil), measured for fork length (FL), weighed, injected with tetracycline hydrochloride (75 mg/kg body weight), and individually marked with visible implant elastomer (VIE) tags (Northwest Marine Technology, Shaw Island, WA). The fish were maintained in a 970 liter flow-through seawater tank for 1 month at ambient water temperature and fed with chopped squid and fish once daily to satiation. After 32 days, the fish were remeasured, reweighed, and their sagittal otoliths were removed for analysis. In addition, 417 YOY juvenile bluefish between 62 and 182 mm FL were collected from southeastern Massachusetts during the years 2004 and 2005 and were used to develop models of the relationship between otolith radius and fork length. ANCOVA was used to compare the slopes of the otolith-size–body-size relationship between wild fish and experimental fish to determine if the experimental conditions caused uncoupling of the relationship.

Otoliths were prepared for analysis as in Oliveira (1996) with two modifications; a 0.48-mm section was cut through the nucleus and visibility of the microstructure was enhanced by soaking the section in trypsin solution. Cross-sectioned bluefish otoliths have an occluded area in the center which obscures observation of the microstructure of the otolith. To clear this region, a procedure was developed in which the sections were placed in 2% trypsin solution for approximately 48 to 72 hours to remove excess protein. This procedure cleared the masked area and enhanced visibility of the rings.

Otoliths were observed on a computer monitor at 100× magnification so that the entire otolith from primordia to ventral edge could be viewed. Measurements were taken by using the Image-Pro Plus 5.0 image analysis software (Media Cybernetics, Silver Spring, MD). Two radial measurements were made on each otolith. The first measurement, R_c, was defined as the distance from the primordium to the ventral edge of the otolith (Fig. 1) and represents the radius of the otolith at the end of the experiment. Because bluefish otoliths develop a curvature that increases

Manuscript submitted 8 May 2006
to the Scientific Editor's Office.

Manuscript approved for publication
13 October 2006 by the Scientific Editor.

Fish. Bull. 105:305–309 (2007).

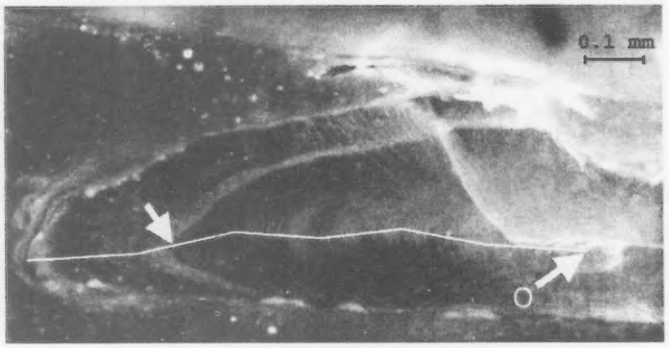


Figure 1

Transverse section of a tetracycline-marked otolith from a juvenile bluefish (*Pomatomus saltatrix*) 32 days from marking viewed with reflected UV light. The white line indicates the axis of fastest growth and indicates the total radius (R_c). The arrow indicates the tetracycline mark. The line segment from the origin (O) to the arrow is the radius of the otolith at the beginning of the experiment (R_i).

with age, a straight line measurement from nucleus to edge would not reflect the true radius and therefore would bias the estimation of growth increments associated with the curvatures. In order to account for this curvature, radial measurements were made along the axis of fastest growth, which was the sum of several straight line measurements from the nucleus to the edge. The second measurement, R_i, was defined as the distance from the primordium to the inner edge of the tetracycline mark deposited on the otolith, along the axis of fastest growth, and represents the radius of the otolith at the time of injection.

The frequency of ring deposition was also determined. The sectioned otoliths were observed at 400× magnification under reflected UV light. When necessary, computer images were enhanced by alternating changes in contrast, and further digital magnification was used to observe rings. The tetracycline mark was located and then the UV light was turned off and the number of rings between the tetracycline-marked ring to the edge of the otolith were counted in normal transmitted light. Two replicates were made for otolith daily ring counts.

Back-calculation formulae

Growth rates from bluefish were estimated by using four back-calculation growth models as described in Francis (1990). In these equations, L_i is the initial fork length of the fish and L_c is the fork length of the fish at the end of the experiment.

The Dahl-Lea equation (based on the study of Lea [1910]) is a simple linear ratio of scale growth to body growth, with the assumption that the two are in exact proportion.

$$L_i = L_c\left(\frac{R_i}{R_c}\right). \tag{1}$$

The Fraser-Lee equation (based on the approach described by Fraser [1916]) is similar to the Dahl-Lea equation but with the Fraser-Lee equation there is the assumption that each back-calculation line passes through the point c, resulting in Equation 2. The value c was calculated as the intercept of the regression of otolith radius and body length (Fig. 2).

$$L_i = c+(L_c-c)\left(\frac{R_i}{R_c}\right). \tag{2}$$

With the SPH (Whitney and Carlander, 1956) there is the assumption of a constant proportional deviation from the mean in scale size such that if the scale is ten percent larger than average for a fish of that length, then it will be ten percent larger throughout the life of the fish. The a and b values for the SPH were calculated as the intercept and the slope of the regression of otolith radius (y) against fork length (x) (Fig. 2). In its linear form, the SPH is expressed as follows:

$$L_i = \left(\frac{-a}{b}\right)+\left(L_c+\frac{a}{b}\right)\left(\frac{R_i}{R_c}\right). \tag{3}$$

The BPH (Whitney and Carlander, 1956) is similar in principal to the SPH but carries that assumption that if a fish is ten percent smaller than an average fish with that size scale, it will be ten percent smaller throughout its life. For the BPH, c is as in Equation 2 and d was

calculated as the slope of fork length (y) plotted against otolith radius (x). In linear form the BPH is expressed as follows:

$$L_i = L_c\left(\frac{c+dR_i}{c+dR_c}\right). \quad (4)$$

The otolith radii and fork lengths were fitted to linear, quadratic, and cubic regression models. The data fitted all the models similarly: r^2 for the linear and quadratic functions were 0.86 and the cubic function had an r^2 of 0.85. A visual comparison of residuals between linear and nonlinear models showed the data to be homoscedastic and therefore the linear model was chosen because of its parsimony. Using these formulae, we estimated the lengths of individual bluefish at the start of the experiment and then compared our estimates to the actual measured lengths. The best model for estimating growth was determined by using paired t-tests. All statistical analyses were made with SPSS, vers. 13.0 (SPSS, Inc., Chicago, IL). For all comparisons $P<0.05$ was considered significant.

Results

Seventy-seven fish were injected with tetracycline and 13 produced readable otoliths that could be used for age and growth analyses. Mortality was high in the first day of the experiment when 26 fish died. Five fish that appeared to be diseased were also removed from the experiment. An additional 21 fish that survived did not show the tetracycline mark and 12 fish had unreadable otoliths. Growth increments were distinguishable and the number of observed rings after the tetracycline injection was within 5% of the number of days in captivity for all tetracycline-injected fish. All replicate counts were within two days of the number of days in captivity.

Some fish died before the 32-day intended experimental time period, and two distinct groups of fish that died were evident. Group 1 included the seven fish that survived at least three weeks (23–32 days) and group 2 included the six fish which lived one week or less (3–7 days). Group 2 did not survive the entire study period but did have the same growth patterns as group-1 fish. For this reason, the data were analyzed as 1) pooled data (all 13 fish), and 2) data from group 1 (7 fish).

Measured growth estimates from all fish varied between 0.4 and 3.0 mm FL/day (Table 1). There was no significant difference ($P=0.13$) in otolith growth rates and body growth rates for the wild fish used to develop the BCFs and the experimental fish, indicating that uncoupling of the relationship did not occur under experimental conditions.

The closest estimate of the measured L_i came from the Dahl-Lea equation, showing no significant difference ($P=0.48$) between the estimates and the initial lengths of the bluefish. The estimates from the Fraser-Lee equation, BPH, and SPH were all significantly different from the measured initial length ($P<0.01$). The

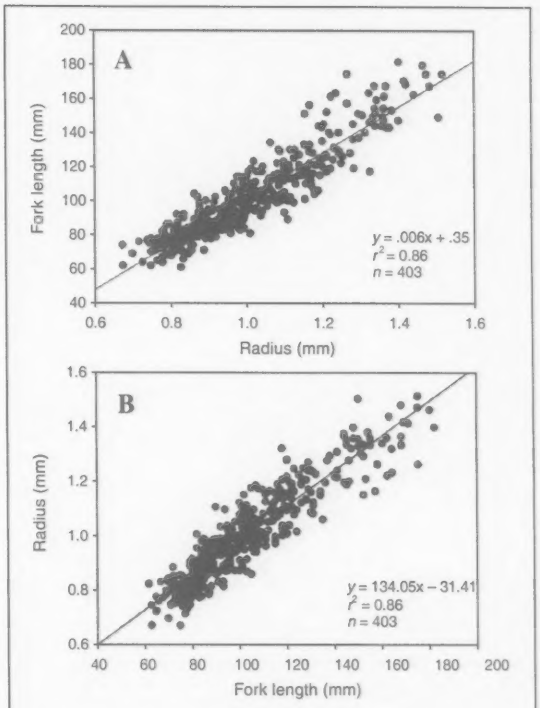


Figure 2

Linear regressions of the somatic-otolith relationship for 403 juvenile bluefish (*Pomatomus saltatrix*) from southeastern Massachusetts: (**A**) Fork length from otolith radius; (**B**) Otolith radius from fork length.

Dahl-Lea equation estimated the L_i by a mean absolute difference of 2.0% ±0.6 standard error (SE) and had a tendency to over-estimate the initial lengths. The Fraser-Lee equation and the BPH were similar in their estimations, tending to under-estimate length by 2.9% ±0.9 SE and 3.0% ±0.9, respectively. The SPH underestimated lengths by a mean of 5.3% ±1.4 SE.

Our analysis of the same data without group-2 fish produced results similar to the results with the pooled data. The Dahl-Lea equation estimations were not significantly different from the L_i ($P=0.41$), whereas the other three equations were significantly different from the measured length (≤ 0.02). Percent differences for all the equations were slightly higher for group-1 fish alone than for the pooled fish. Dahl-Lea estimates differed from the measured lengths by 3.1% ±0.9 SE, the Fraser-Lee and BPH estimates both differed by 4.7% ±1.3 SE, and the SPH differed by 8.6% ±1.7 SE.

Discussion

The agreement between the number of daily rings and the days after injection indicates that the observed ring

Table 1

Summary of variables and back-calculation equation results for tetracycline-injected juvenile bluefish (*Pomatomus saltatrix*). BPH = body proportional hypothesis, SPH = scale proportional hypothesis, L_i = initial fork length of fish, L_f = final fork length of fish, R_i = initial radius of otolith, and R_f = final radius of otolith. * Indicates a significant difference from the measured initial fork length (L_i) ($P<0.05$).

Fish number	Days after injection	L_i	L_f	Growth (mm)	Growth rate (mm/day)	R_f	R_i	Dahl-Lea	Fraser-Lee*	BPH*	SPH*
1	32	84.0	116.0	32.0	1.0	1.0	0.8	86.1	78.0	77.3	72.2
2	32	89.0	120.0	31.0	1.0	1.2	0.9	94.6	87.9	88.1	83.1
3	32	89.0	112.0	23.0	0.7	0.9	0.7	94.6	89.6	88.2	86.1
4	25	91.0	105.0	14.0	0.6	1.1	0.9	88.7	83.7	84.3	80.3
5	23	93.0	102.0	9.0	0.4	1.0	0.9	92.9	90.1	90.1	88.1
6	23	93.0	108.0	15.0	0.7	1.0	0.8	89.7	84.4	84.0	80.6
7	23	101.0	115.0	14.0	0.6	1.1	0.9	101.6	97.9	97.8	95.3
8	7	118.0	121.0	3.0	0.4	1.2	1.2	118.2	117.5	117.6	117.0
9	4	122.0	125.0	3.0	0.8	1.2	1.1	122.2	121.5	121.5	121.0
10	4	128.0	130.0	2.0	0.5	1.1	1.1	127.7	127.1	127.1	126.7
11	3	127.0	129.0	2.0	0.7	1.2	1.2	126.4	125.7	125.7	125.2
12	3	118.0	127.0	9.0	3.0	1.2	1.1	119.7	117.8	117.8	116.6
13	3	133.0	136.0	3.0	1.0	1.1	1.0	130.8	129.6	129.3	128.7
Mean		106.6	118.9	12.3	0.9			107.2	103.9	103.8	101.6

formation occurred daily. This is in agreement with Nyman and Conover (1988) who used tetracycline to validate that rings were formed daily in juvenile bluefish. This finding indicates that the tetracycline mark was formed directly after the injection and that the number of rings, after tetracycline marking, corresponded with the number of days in the study period.

The Dahl-Lea equation provided the most accurate estimate of the initial size of the bluefish at the start of the experiment. This is the simplest equation and is based solely on the linearity of the otolith-size–body-size relationship. The accuracy of the estimation may be due to bluefish being a fast growing species. Wright et al. (1990) found that faster growing salmon smolts fit a linear growth model more favorably than slower growing conspecifics. It is possible that daily otolith growth is conservative, to a certain extent, as found by Panfili and Tomás (2001), but that the width of the daily growth increments may be a function of metabolism as postulated by Wright et al. (1990) or a function of temperature (Mosegaard et al., 1988). Therefore, species with high metabolisms, such as bluefish, may be expected to show a more direct relationship between otolith growth and somatic growth than a fish with a slower metabolism.

The Fraser-Lee equation underestimated the true initial lengths of the fish by a mean of 2.8%. This underestimate may be due the length-intercept constant c in the to the Fraser-Lee equation. When this constant is given a biological interpretation of zero, the equation is the same as the Dahl-Lea equation; therefore the interpretation of c is important in determining the accuracy of the Fraser-Lee and BPH equations. The c calculated by the linear regression was a negative value, −31.41; the underestimation was likely caused by changes in the otolith-size–body-size relationship during different life stages.

Hare and Cowen (1997) found significant differences between different ontogenetic stages during the bluefish larval period. These differences would explain why the regression of the otolith radius on fork length data did not predict a biologically reasonable y-intercept, although the data were strongly linear: the ratios during the juvenile and larval stages were different. When applying BCFs a biological intercept may be more useful and could make the Fraser-Lee BCF the more accurate equation. However, because otolith formation occurs during the early egg stage (0–24 hours) (Hare and Cowen, 1994), it would be problematic to get an accurate mean length at time of formation. Given that this measurement is likely to be less than the 2.0–2.4 mm hatching size (Klein-MacPhee, 2002) and that the otolith growth to somatic growth relationship is linear, forcing an intercept of zero should provide reasonably accurate length estimations.

In summary, this study was designed to validate and compare back-calculation methods for a fast growing juvenile bluefish, rather than to characterize bluefish growth. All four back-calculation formulae did result in close estimates (≤8.6%) of the true initial length regardless of growth rate (0.4 to 3.0 mm FL/day). Although the sample sizes were not adequate to properly explore the observed variability in growth rate the fact that the precision of the BCFs was not affected by growth rate illustrates a link between the rate of otolith growth and body growth, at least in the short term. In the case of bluefish, the results of this study indicate that the relationship between otolith growth

and body growth is linear for juveniles. The Dahl-Lea equation is the most parsimonious BCF equation and best approximated the true growth rate of juvenile bluefish, therefore making it the best suited method for estimating growth rate during the juvenile phase of this species. However it should be noted that the linear model used to develop the BCFs may not hold true for larval development or for annual growth of adults; more complex models may be needed to accurately estimate the amount of growth beyond year one. Caution must also be used in applying the equation because the lack of significant difference between the Dahl-Lea–predicted lengths and true initial lengths of the fish may have been due to the small sample size. If the linear relationship between somatic and otolith growth is, in fact, influenced by growth rate, then the Dahl-Lea equation may prove to be useful in back-calculating length for other fast-growing species of fishes.

Acknowledgments

This research was funded by the National Marine Fisheries Service/CMER grant no. NOAA Ref. NA04NMF4550380. We thank T. Rajaniemi for her advice and assistance with statistical analysis and S. Cadrin for reading an earlier draft of this manuscript.

Literature cited

Fahay, M. P., P. L. Berrien, D. L. Johnson, and W. W. Morse.
1999. Essential fish habitat source document: Bluefish, *Pomatomus saltatrix*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-144, 68 p.

Francis, R. I. C. C.
1990. Back-calculation of fish length: a critical review. J. Fish Biol. 36:883–902.

Fraser, C. Mcl.
1916. Growth of the spring salmon. Trans. Pacif. Fish. Soc. 1915:29–39.

Hare, J. A., and R. K. Cowen.
1994. Ontogeny and otolith microstructure of bluefish *Pomatomus saltatrix* (Pisces: Pomatomidae). Mar. Biol. 118:541–550.
1995. Effect of age, growth rate, and ontogeny on the otolith size-fish size relationship in bluefish, *Pomatomus saltatrix*, and the implications for back-calculation of size in fish early life history stages. Can. J. Fish. Aquat. Sci. 52:1909–1922.
1997. Size, growth, development, and survival of the planktonic larvae of *Pomatomus saltatrix* (Pisces: Pomatomidae). Ecology 78:2415–2431.

Kendall, A. W. Jr., and L. A. Walford.
1979. Sources and distribution of bluefish, *Pomatomus saltatrix*, larvae and juveniles off the east coast of the United States. Fish. Bull. 77:213–227.

Klein-MacPhee, G.
2002. Bluefish. Family Pomatomidae. *In* Bigelow and Schroeder's Fishes of the Gulf of Maine, 3rd ed. (B. B. Collette, and G. MacPhee, eds.), p. 400–406. Smithsonian Institution Press, Washington, DC.

Lea, E.
1910. On the methods used in the herring-investigations. Con. Perm. Int. L'explor. Mer 53:7–174.

Mosegaard, H., H. Svedang, and K. Taberman.
1988. Uncoupling of somatic and otolith growth rates in Atlantic char (*Salvelinus alpinus*) as an effect of differences in temperature response. Can. J. Fish. Aquat. Sci. 45:1514–1524.

Munch, S. B., and D. O. Conover.
2000. Recruitment dynamics of bluefish (*Pomatomus saltatrix*) from Cape Hatteras to Cape Cod, 1973–1995. ICES J. Mar. Sci. 57:393–402.

Nyman, R. M., and D. O. Conover.
1988. The relation between spawning season and the recruitment of young-of-the-year bluefish, *Pomatomus saltatrix*, to New York. Fish. Bull. 86:237–250.

Oliveira, K.
1996. Field validation of annular growth rings in the American eel, *Anguilla rostrata*, using tetracycline-marked otoliths. Fish. Bull. 94:186–189.

Panfili, J., and J. Tomás.
2001. Validation of age estimation and back-calculation of fish length based on otolith microstructures in tilapias (Pisces, Cichlidae). Fish. Bull. 99:139–150.

Whitney, R. R., and K. D. Carlander.
1956. Interpretation of body-scale regression for computing body length of fish. J. Wild. Mgmt. 20:21–27.

Wright, P. J., N. B. Metcalfe, and J. E. Thorpe.
1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. J. Fish Biol. 36:241–249.

Fishery Bulletin

Guidelines for authors

Content of manuscripts

Contributions published in Fishery Bulletin describe original research in marine fishery science, fishery engineering and economics, as well as the areas of marine environmental and ecological sciences (including modeling). Although all contributions are subject to peer review, responsibility for the contents of papers rests upon the authors and not upon the editor or publisher. *Submission of an article implies that the article is original and is not being considered for publication elsewhere.* Manuscripts must be written in English. Authors whose native language is not English are strongly advised to have their manuscripts checked by English-speaking colleagues prior to submission. **Articles** may range from relatively short contributions (10–15 typed, double-spaced pages, tables and figures not included) to extensive contributions (20–30 typed pages). **Notes** are reports of 5 to 10 pages without an abstract and describe methods or results not supported by a large body of data.

Manuscript preparation

Title page should include authors' full names and mailing addresses and the senior author's telephone, fax number, and e-mail address, and a list of key words to describe the contents of the manuscript. **Abstract** should be limited to 150 words (one-half typed page), state the main scope of the research, and emphasize the author's conclusions and relevant findings. Do not review the methods of the study or list the contents of the paper. Because abstracts are circulated by abstracting agencies, it is important that they represent the research clearly and concisely. **Text** must be typed in 12 point Times New Roman font throughout. A brief introduction should convey the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods, Results, Discussion (or Conclusions),** and **Acknowledgments**. Headings within each section must be short, reflect a logical sequence, and follow the rules of multiple subdivision (i.e., there can be no subdivision without at least two items). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be written out in full the first time they are used. Include FAO common names for species in the list of keywords and in the introduction. Regional common names may be used throughout the rest of the text if they are different from FAO common names which can be found at http://www.fishbase.org/search.html. Follow the U.S. Government Printing Office Style Manual (1984 ed.) and the CBE Style Manual (6th ed.) for editorial style; for fish nomenclature follow the most current issue of the American Fisheries Society's Common and Scientific Names of Fishes from the United States and Canada. Dates should be written as follows: 11 November 2000. Measurements should be expressed in metric units, e.g., 58 metric tons (t); if other units of measurement are used, please make this fact explicit to the reader. Write out the numbers zero through nine unless they form part of measurement units (e.g., nine fish but 9 mm).

Text footnotes should be inserted in 9-point font at the bottom of the page that displays the first citation of the footnote. Footnotes should be formatted in the same manner as citations. Footnote all personal communications, unpublished data, and unpublished manuscripts with full address of the communicator or author, or, as in the case of unpublished data, where the data are on file. Authors are advised to avoid references to nonstandard (gray) literature (such as internal, project, processed, or administrative reports, ICES Council Minutes, IWC Minutes or Working Papers, any "research" or "working" documents, laboratory or contract reports, Management Council reports, and manuscripts in review) wherever possible. If these references are used, present them as footnotes and list whether they are available at NTIS (National Technical Information Service) or at some other public depository. Cite all software and special equipment or chemical solutions used in the study, not in a footnote but within parentheses in the text (e.g., SAS, vers. 6.03, SAS Inst., Inc., Cary, NC).

Literature cited comprises published works and those accepted for publication in peer-reviewed literature (in press). Follow the name and year system for citation format in the "Literature cited" section. If there is a sequence of citations in the text, list chronologically: (Smith, 1932; Green, 1947; Smith and Jones, 1985). Abbreviations of serials should conform to abbreviations given in the Serial Sources for the BIOSIS Previews Database. Authors are responsible for the accuracy and completeness of all citations. Literature citation format: Author (last name, followed by first-name initials). Year. Title of report or manuscript. Abbreviated title of the series to which it belongs. Always include number of pages. If the authorship for a sequence of citations is identical, list works chronologically.

Tables and figures—general format

- Zeros should precede all decimal points for values less than one.
- Sample size, n, should be italicized.
- Capitalize the first letter of the first word in all labels within figures.
- Do not use overly large font sizes in maps and for units of measurements along axes in figures.
- Do not use bold fonts or bold lines in figures.
- Do not place outline rules around graphs.
- Do not use horizontal lines in graphs to indicate measurement units on axes.
- Use a comma in numbers of five digits or more (e.g. 13,000 but 3000).
- Maps should have a North arrow (or compass sign) and degrees latitude-longitude (e.g., 170°E)

Tables are often overused in scientific papers; it is seldom necessary or even desirable to present all the data associated with a study. Tables should not be excessive in size and must be cited in numerical order in the text. Headings should be short but ample enough to allow the table to be intelligible on its own. All unusual symbols must be explained in the table legend. Other incidental comments may be footnoted with italic footnote markers. Use asterisks to indicate probability in statistical data. Do not type table legends on a separate page; place them on the same page as the table data. *Do not submit tables in photo mode.*

Figures include line illustrations, photographs (or slides), and computer-generated graphs and must be cited in numerical order in the text. Graphics will aid in the comprehension of the text, but they should be limited to presenting patterns rather than raw data. Figures are costly to print and should be limited to six. Figures must be labeled with author's name and number of figure. Avoid placing labels vertically (except on *y*-axis). Figure legends should explain all symbols and abbreviations and should be double-spaced on a separate page at the end of the manuscript. Please note that we do not print graphs in color.

FAILURE TO FOLLOW THESE GUIDELINES WILL DELAY PUBLICATION OF A MANUSCRIPT

Copyright law does not apply to *Fishery Bulletin*, which falls within the public domain. However, if an author reproduces any part of an article from *Fishery Bulletin* in his or her work, reference to source is considered correct form (e.g., Source: Fish. Bull 97:105).

Reprints are available free of charge to the senior author (50 copies) and to his or her laboratory (50 copies).

Submission

The Scientific Editorial Office encourages authors to submit their manuscripts as a *single* PDF (preferred), or Word (zipped) document by e-mail to Fishery.Bulletin@noaa.gov. Please use the subject heading "Fishery Bulletin manuscript submission." *Do not* send encrypted files. For further details on electronic submission, please contact the Scientific Editorial Office directly (see address below). Or you may send your manuscript on compact disc in one of the above formats along with four printed copies (one original plus three copies [stapled]) to the Scientific Editor, at the address shown below.

Dr. Adam Moles
Scientific Editor, *Fishery Bulletin*
11305 Glacier Hwy
Juneau, AK 99801-8626

Once the manuscript has been accepted for publication, you will be asked to submit a final software copy of your manuscript. When requested, the text and tables should be submitted in Word or Word Rich Text Format. Figures should be sent as PDF files, Windows metafiles, tiff files, or as EPS files. Send a copy of figures in original software if conversion to any of these formats yields a degraded version.

Announcement of the NMFS (National Marine Fisheries Service) best paper awards

The National Marine Fisheries Service best scientific paper awards for 2006 were awarded to the following authors:

Butler, John, Melissa Neuman, Deanna Pinkard, Rikk Kvitek, and Guy Cochrane

The use of multibeam sonar mapping techniques to refine population estimates of the endangered white abalone (*Haliotis sorenseni*)

Fishery Bulletin 104:521–532

Maloney, Nancy E.

Sablefish, *Anaplopoma fimbria*, populations on Gulf of Alaska seamounts

Marine Fisheries Review 66(3):1–12

Fishery Bulletin

Subscription form

Superintendent of Documents **Publications** Order Form

*5178

☐ YES, please send me the following publications:

____ Subscriptions to *Fishery Bulletin*
for $36.00 per year ($50.40 foreign)

The total cost of my order is $ _____ . Prices include regular domestic postage and handling and are subject to change.

_____
(Company or Personal Name) (Please type or print)

_____
(Additional address/attention line)

_____
(Street address)

_____
(City, State, ZIP Code)

_____
(Daytime phone including area code)

_____
(Purchase Order No.)

Charge your order. IT'S EASY!

VISA

MasterCard

Please Choose Method of Payment:

☐ Check Payable to the Superintendent of Documents

☐ GPO Deposit Account ☐☐☐☐☐☐☐–☐

☐ VISA or MasterCard Account

☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐☐

☐☐☐☐ (Credit card expiration date)

To fax your orders (202) 512-2250

_____
(Authorizing Signature)

Thank you for your order!

Mail To: Superintendent of Documents
P.O. Box 371954, Pittsburgh, PA 15250-7954

Also available online at http://bookstore.gpo.gov/collections/fishery-bulletin